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Austral Hepaticae 45. A Monograph of the Genus *Chiloscyphus* Corda (Lophocoleaceae) for Australasia

John J. Engel

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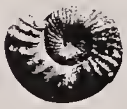

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Dedicated to
Karen Ruth Engel

Austral Hepaticae 45. A Monograph of the Genus *Chiloscyphus* Corda (Lophocoleaceae) for Australasia

John J. Engel

Abstract

Chiloscyphus is the largest genus of Lophocoleaceae and has ca. 250 species. In this monograph, 38 species are recognized for Australasia. Included are two new species and two new varieties. Six subgenera are recognized for Australasia: subg. *Notholophocolea* (R. M. Schust.) J. J. Engel & R. M. Schust., including sect. *Notholophocolea* J. J. Engel, sect. nov.; subg. *Lophocolea* (Dumort.) J. J. Engel & R. M. Schust.; subg. *Connati* (Lindenb.) J. J. Engel, including sect. *Connati* (Lindenb.) J. J. Engel, comb. nov.; subg. *Microlophocolea* (Spruce) J. J. Engel; subg. *Septati* Engel, subg. nov.; and subg. *Spinoscyphus* J. J. Engel, subg. nov. The largest subgenus is *Lophocolea*, with 20 species belonging to four sections (*Lophocolea* (Dumort.) J. Hentschel, *Novae-zeelandii* J. J. Engel, *Semiteres* J. J. Engel, and *Aperticaules* Engel, sect. nov.). Each of the species is described and illustrated. Included are two new species, *C. mediinfrons* J. J. Engel & Braggins, sp. nov., and *C. septatus* J. J. Engel, sp. nov.

Introduction

The Lophocoleaceae consist of five subfamilies: Lophocoleoideae, Leptoscyphoideae, Leptophyllopsoideae, Conoscyphoideae, and Physothecoideae. The family is here recognized as distinct from Geocalycaceae, following Hentschel et al. (2006a), who demonstrated that Lophocoleaceae and Geocalycaceae are two independent families on the basis of molecular evidence coupled with characters derived from the female inflorescence. The Leptoscyphoideae consist of eight genera; all but one are monotypic. *Evansianthus* R. M. Schust. & J. J. Engel, with *E. georgiensis* (Gottsche) R. M. Schust. & J. J. Engel, is Antarctic in distribution (Schuster and Engel, 1973; Engel, 1990a). *Bragginsella* R. M. Schust. of New Zealand, with only *B. anomala* R. M. Schust., was originally placed in Jungermanniaceae subfam. Jungermannioideae (Schuster, 1997a) and treated immediately before the genus *Jungermannia* by Schuster (2002), but, on the basis of evidence derived from the gynoecium, the genus belongs in Lophocoleaceae (David Glenny, in litt.). *Lamellocolea* J. J. Engel, with only *L. granditexta* (Steph.) J. J. Engel, is endemic to New Zealand (Engel, 1991c). *Leptoscyphopsis* R. M. Schust., with only *L. paradoxus* R. M. Schust., occurs at high elevations in the Venezuelan Andes (Estado Mérida; see Schuster, 1978, 1998; Gradstein et al., 2001). *Pedinophyllopsis* R. M. Schust. & Inoue, with *P. abditus* (Sull.) R. M. Schust. & Inoue, is a subantarctic species that ranges into southern South America (see Schuster and Engel, 1981, 1982; Engel, 1990a). *Platycaulis* R. M. Schust. has only *P. renifolius* R. M. Schust. of the Venezuelan Andes (Páramo de Tamá, Estado Mérida; see Schuster, 1978, 1995). *Pseudolophocolea* R. M. Schust. & J. J. Engel, contains only the New Zealand *P. denticulata* (Schuster and Engel, 1981, 1982). *Leptoscyphus* Mitt. is larger and has ca. 25 species concentrated in tropical and south temperate areas (cf. Grolle, 1962); several species occur in Australasia. The Leptoscyphoideae were reviewed in Schuster and Engel (1982).

The Lophocoleoideae are larger and comprise 10 genera. Some are monotypic. *Pigafettoa* C. Massal. has only *P. crenulata* C. Massal. of southern South America and the Falkland Islands (Engel and Schuster, 1974; cf. Engel, 1990a). *Perdusenia* Hässel, has a single species, *P. rheophila* Hässel, of southern South America (Hässel de Menéndez, 1989), and *Xenocephalozia* R. M. Schust. has the southern South American *X. navicularis* (Steph.) R. M. Schust. (Schuster, 1965). The subfamily also contains several small genera. *Stolonivector* J. J. Engel has four species, all from New Zealand (Engel, 1991a, 2003, 2009). *Hepatostolonophora* J. J. Engel & R. M. Schust. has two species in southern South America and two in Australasia (Engel, 1979). *Pachyglossa* Herzog & Grolle, with four species, is south temperate–subantarctic (Herzog and Grolle, 1958).

Three genera of the Lophocoleoideae are markedly larger. *Heteroscyphus* Schiffn. (incl. *Tetracymbaliella* Grolle; see Engel and Schuster, 1985) has ca. 75 species and is primarily south temperate and tropical in distribution. *Clasmatocolea* Spruce, has 19 species, mostly south temperate in distribution (Engel, 1980). *Chiloscyphus* Corda is the largest genus in the family and has ca. 250 species, although that number is purely a rough estimate. The genus, as recognized here, includes *Lophocolea*. Engel and Schuster (1985) discussed *Chiloscyphus* and *Lophocolea* on a world-wide basis, enumerated in detail all characters that had been used to differentiate the two genera, and concluded the two genera cannot be maintained. Engel and Schuster (1985) placed *Lophocolea* as a subgenus of *Chiloscyphus* (the formal placement was made in Engel [1998]). Several other studies, on the basis of molecular evidence, concluded that *Chiloscyphus* and *Lophocolea* are congeneric, such as He-Nygrén and Piippo (2003), Hentschel et al. (2006a,b). Engel and Schuster (1985) also included a discussion of the conceptual history of the use of *Chiloscyphus*, *Lophocolea*, and also *Heteroscyphus*, and especially the use of these genera in south temperate and subantarctic areas.

Subfamily Leptophyllopsoideae J. J. Engel has one genus, *Leptophyllopsis* R. M. Schust. Two species belong here: one in Australasia, *L. laxus* (Mitt.) R. M. Schust., the other in southern South America, *L. irregularis* (Steph.) J. J. Engel (see Engel, 2007).

Subfamily Conoscyphoideae J. J. Engel, contains only the monotypic *Conoscyphus* Mitt. *Conoscyphus trapezioides* (Sande Lac.) Schiffn. occurs in Queensland, Australia (Engel, 1987), Samoa, Solomon Islands, New Guinea, north in Indonesia to Malacca, and also the Mascarenes, Cameroon Mtn., and St. Thomé. *Conoscyphus tjiwideiensis* (Sande-Lac.) Schiffn. belongs to *Acroscyphella* N. Kitag. & Grolle, as *A. tjiwideiensis* (Sande-Lac.) N. Kitag. & Grolle (see Kitagawa and Grolle, 1985).

Subfamily Physothecoideae J. J. Engel & Gradst. is monotypic, with only *Physotheca autoica* J. J. Engel & Gradst. (Engel and Gradstein, 2003), known only from a small area in the Eastern Cordillera of the Andes of southern Ecuador.

The present monograph, encompassing some 38 species of *Chiloscyphus*, is part of continuing monographic research on Australasian Lophocoleaceae. Plants of this genus (including *Lophocolea*) are notorious for their pronounced plasticity and difficulty. Scott (1985, p. 139), for example, commented that *Lophocolea* is "one of the largest and, at least in my experience, one of the most difficult genera...." A half century ago, two authors independently made quite apt remarks in the same year. Jones (1953) commented on African representatives of *Lophocolea*, but the following remarks apply to a taxonomic study of this group in any part of the world.

> The species of *Lophocolea* are exceptionally plastic, and a considerable number of the species and varieties which have been described in the past have come to be recognized as mere growth-forms.... It is difficult to find any stable characters on which to base the separation of species, even those characters of undoubted systematic value being liable to vary greatly within the limits of a single gathering, and often, indeed, of a single stem; if any description is to be accurate, almost everything must be qualified by adverbs such as 'usually,' 'normally,' or 'locally,' and if any clear conception of a species is to be gained, populations, not single stems, must be studied. Under these conditions, it is almost inevitable that a fairly broad conception of the species should be adopted; that ecotypes or geographical races of the more widespread species exist seems highly probable; that they can be distinguished by herbarium studies alone seems highly improbable. (Jones, 1953, p. 172)

Remarks of Hodgson (1953, p. 329), in a study of New Zealand representatives, are similar: "It is with much trepidation that one undertakes the revision of a genus such as *Lophocolea*, and one encounters expected difficulties almost from the outset. In New Zealand the species are so variable and in such a fluid state, and the interrelations within certain groups are so manifest, that with the Old World conception of a species being what it is, it is no wonder that the number of described species has reached at least 50, not including those already synonymized by Mitten." Hodgson (1953) recognized 31 species of *Lophocolea*, but it should be mentioned that her concept of that genus included elements that were later shown to belong to various other genera. For example, *L. notophylla* was placed in *Clasmatocolea* (Grolle, 1960; Engel, 1980); *L. fiordlandiae* was placed in *Stolonivector* (Engel, 1991a, 2003); *L. paucistipula* was transferred to *Hepatostolonophora* (Engel, 1979); and *L. biciliata* was shown to belong to *Heteroscyphus* (Engel, 1991c).

The difficulties enumerated by earlier authors are real, and the result is a widespread misuse of names, with numerous misidentifications in herbaria, as well as the unnecessary introduction of many names into the literature. My approach to these problems included two primary components. Attempts were made to examine and understand populations in the field in New Zealand, Tasmania, and southeast Australia. This included oil-body studies of as many species as possible. The study also included examination of thousands of dried herbarium specimens, among them the collections of Engel, Schuster, Child, Hatcher, Allison, and Hodgson. Also included are the specimens on deposit at Landcare in Lincoln, New Zealand, as well as those in Hobart, Tasmania. All of the relevant type specimens were studied.

I attempted to document the variability of Australasian taxa by including, wherever possible, discussions, illustrations, and, at times, graphs and charts. Also, I believe that it is essential, in a study such as this, that discussions include comments on type specimens, especially as they relate to the variation spectrum of the accepted taxon. I therefore have included a short discussion of most types under the head "Notes on Type Specimens;" this section immediately follows the "Notes" or "Variation" section. Various other comments on the type also are included, especially those relevant to typification.

This extensive study has resulted in a considerable refinement of species concepts as well as acceptance of several taxa not previously recognized. For purposes of ease of use, a key to the subgenera and sections is initially presented, and, under each subgenus and section, the relevant species are keyed.

Taxonomic Characters, Morphology, and Terminology

The genus *Chiloscyphus* has an abundance of taxonomic characters. Some of these characters are unique to the genus and, interestingly, in a number of instances, are restricted to Australasian representatives of the genus. For example, leaf surface tubercles occur in *Chiloscyphus* only in the Australasian sect. *Leucophylli*. A leaf-free strip of stem cells occurs only in a few species of the genus, all Australasian, and septate rhizoids are present only in one species endemic to New Zealand. These features will be enumerated in the following discussions of the various morphological characters.

PLANT SIZE—As with many hepatics, plant size is frequently correlated with habitat. However, often a particular size range is characteristic of the species. For example, *Chiloscyphus muricatus* is a small species, and, when diminutive, plants need to be searched for with care in the field. On the other hand, *C. mittenianus* of New Zealand and *C. suboppositus* of Tasmania are among the larger representatives and are more easily recognized in the field. It should be noted that the shoot width was made by measuring the main shoot without altering the leaf orientation, i.e., without spreading the leaves.

BRANCHING—Branching patterns within regional *Chiloscyphus* taxa are of considerable taxonomic significance. My study of branch types is based on detailed examination of numerous different collections of each species. Three branch types occur in our species of *Chiloscyphus*, but in variable and fascinating combinations.

Terminal, *Frullania*-type as well as both lateral- and ventral-intercalary–type branches occur in subg. *Notholophocolea*, subg. *Lophocolea* and subg. *Microlophocolea*. However, only *C. austrigenus* (subg. *Notholophocolea*) and *C. villosus* (subg. *Microlophocolea*) have all three branch types common. Ventral-intercalary branches are present but rare in three species of subg. *Lophocolea* (*C. lentus*, *C. longiciliatus*, and *C. bispinosus*). On the other hand, *C. erosus* (subg. *Lophocolea*) has both lateral and ventral-intercalary branches common, and only rarely does it produce terminal branches. Ventral-intercalary branches are present in only two other species, namely, *C. septatus* (subg. *Septati*) and *C. muricatus* (subg. *Microlophocolea*). The first species has branches nearly exclusively intercalary, and the latter two have the combination of ventral-intercalary and terminal branches, with lateral-intercalary branching being absent.

Most of the remaining Australasian *Chiloscyphus* taxa have terminal and lateral-intercalary branches in varying combinations of frequency. A number of taxa, sometimes the primitive taxa in a section, have both branch types common. However, a shift occurs in several sections toward reduction or loss of terminal or lateral-intercalary branches. Each of the three sections of subg. *Lophocolea* has such a shift. For example, in sect. *Lophocolea*, *C. herzogii* and *C. lentus* have both types common, whereas terminal branches tend to prevail in the more derivative taxa, such as *C. subporosus* and *C. cuspidatus*. Two trends toward loss of a branch type occur in sect. *Novarum-zeelandiarum*: one toward loss of lateral-intercalary branches (*C. calcareus*), the other toward loss of terminal branches (*C. hattorii*). A tendency toward loss of terminal branches also occurs in sect. *Semiteres* and sections *Connati* and *Leucophylli* of subg. *Connati*. Branching is nearly exclusively intercalary, with terminal branches very rare in subg. *Septati*.

Lateral-intercalary branches in several taxa vary in position from lateral to ventral–lateral to nearly ventral. Branches that are nearly ventral occur in the lateral half of an underleaf axil and are found in species with plastic intercalary branch position. That variability is documented in the text (e.g., *C. lentus* sub notes), and in such cases, care is needed to distinguish this branch type from true ventral-intercalary branches, which issue from the median sector of an underleaf axil.

LEAVES—The leaf in our species of *Chiloscyphus* on the one hand is plastic yet, on the other hand, is of considerable taxonomic value, offering a significant number of characters.

Orientation is strongly succubous, except in *C. austrigenus* and *C. edentatus*, where it is subtransverse to subsuccubous (Fig. 2: 2, *C. austrigenus*). The insertion at the ventral end varies from no recurvature to slightly recurved and then comma-like to strongly recurved and then J-shaped (Fig. 78: 2, *C. villosus*). The marked recurvature at the ventral end of the insertion line in *C. trichocoleoides* (Fig. 80: 2) is, to my knowledge, unique in the genus. In nearly all species the leaf insertion attains the stem midline dorsally; therefore, no leaf-free strip of stem cells is delimited. *Chiloscyphus excisifolius*, *C. aperticaulis*, and *C. mediinfrons* are the only notable exceptions. The presence vs. absence of a leaf-free strip of stem cells is a reliable taxonomic character, but one that must be studied with care under the compound microscope. However, at times, this procedure does not clearly reveal details of the insertion. In such cases, a shoot should be cut into several pieces, cleared with Hoyers medium, mounted with the dorsal surface exposed, and examined under a compound microscope.

Leaves are often connate dorsally in subg. *Connati*, and particularly strongly so in *C. aculeatus*. Connation tissue in that species is several cells high and forms a trough (Fig. 62: 2).

Leaves may be undivided and entire, as in *C. austrigenus* and several taxa of sect. *Semiteres*, such as *C. fertilis*. Other groups, such as sect. *Lophocolea* and subg. *Connati*, have leaves that are fundamentally bifid. Species with leaves characterized by a variation spectrum that includes both undivided and bifid representatives occur in several subgenera, i.e., subg. *Lophocolea* (*C. novaezeelandiae*, Figs. 29: 2, 3; 30: 7, 8), subg. *Connati* (*C. mittenianus*, Fig. 70: 2, 3) and subg. *Microlophocolea* (*C. gippslandicus*, Fig. 75: 4, 5). In each case the presence of the two character states is of taxonomic value.

Notable leaf surface features are present in three of the five subgenera. The tuberculae are a sectional character for the *Leucophylli* and occur on both surfaces of the leaf, positioned one each per cell over the lumen (Fig. 65: 2, *C. leucophyllus*). Such tuberculae within *Chiloscyphus* are known only from that section. All other Australasian taxa of subg. *Connati* have smooth leaves. Surface echinae occur in subg. *Microlophocolea*, and their distribution and insertion are taxonomically relevant. In sect. *Microlophocolea*, echinae occur on both dorsal and ventral surfaces (Fig. 79: 11, *C. muricatus*), whereas they are restricted to the dorsal surface in sect. *Hemispini* (Fig. 72: 3, *C. parvispineus*). The two sections of subg. *Microlophocolea* each have a species with echinae inserted strictly over the cell lumen (*C. muricatus* of sect. *Microlophocolea*, Fig. 79: 11; *C. parvispineus* of sect. *Hemispini*, Fig. 72: 3). Interestingly, the two sections also each have a species with echinae inserted both over the cell lumen as well as the radial walls (*C. villosus* of sect. *Microlophocolea*, Fig. 77: 3; *C. gippslandicus* of sect. *Hemispini*, Fig. 75: 14, 15). Surface echinae in the family Lophocoleaceae occur on both leaf and stem tissue only in *Cyanolophocolea echinella*.

Leaf margins of most taxa are entire and devoid of any trace of teeth. Several taxa, however, have margins armed with several to numerous teeth, examples being *C. longiciliatus* (sect. *Lophocolea*, Fig. 17: 5), taxa of subg. *Microlophocolea* (Fig. 76: 6, 7, *C. villosus*), and various members of sect. *Leucophylli* (Fig. 70: 1, 2, *C. mittenianus*).

Leaf length vs. width is at times included. In undivided leaves, the length was obtained by measuring a line extending from the median point of the apex to the leaf base. In bifid leaves, that line (B in Fig. 1: 1, 2) extends from the leaf base, through the maximum depth of the sinus, to the bisection with line A (which extends between the lobe apices, Fig. 1: 1, 2). Width was obtained from the widest point of the leaf (Fig. 1: 1, 2, line C). The resulting vertical and horizontal intersecting lines are normally at 90°, but slight deviations from 90° occasionally result due to leaf shape. Such deviations involve only minor differences in width measurements.

LEAF CELLS—Leaf cells provide a number of taxonomic characters.

Cell size is a diagnostic or taxonomically useful character for several species. *Chiloscyphus muricatus* has small cells,

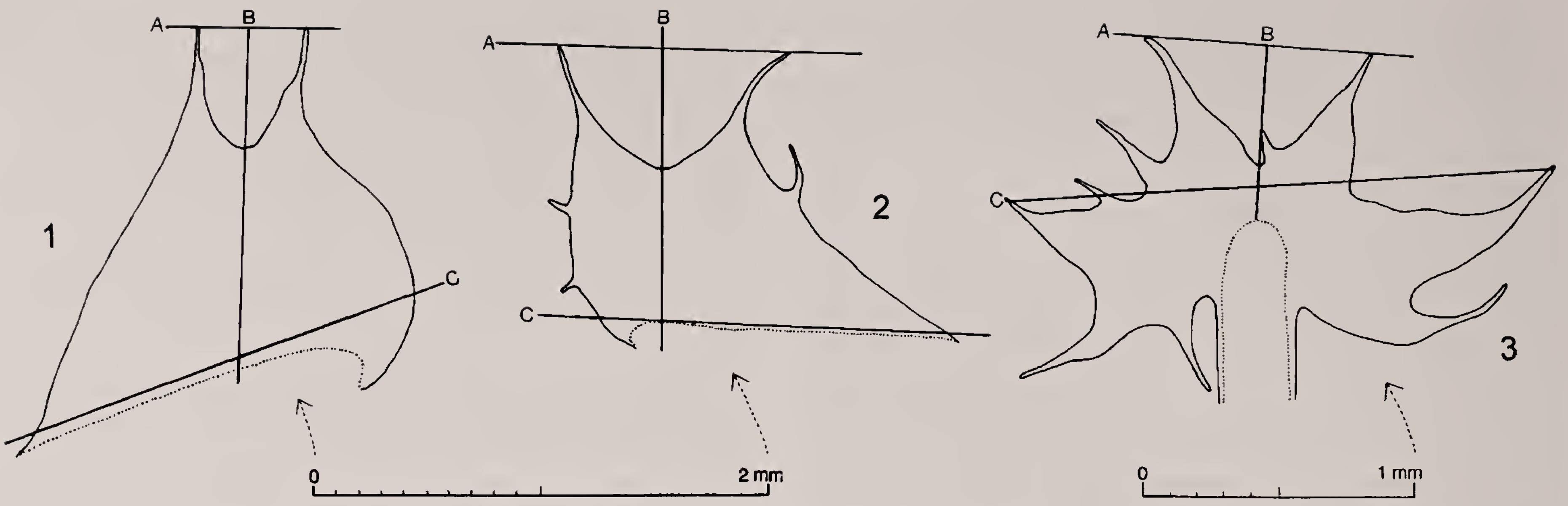

FIG. 1. Leaves and underleaf showing loci of measurements. **1, 2.** *Chiloscyphus bispinosus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **3.** *C. spinifer* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. (For explanation, see text.)

whereas *C. villosus*, of the same section, has larger cells. Likewise, the larger cells of *C. multipennus* distinguish that species from its ally, *C. helmsianus*. Similarly, the larger cell size of *C. cuspidatus* is a useful taxonomic character to distinguish that species from the smaller celled *C. lentus*. Cells were measured, unless otherwise stated, in the median sector of the leaf.

A few species have dimorphic leaf cells; these are of four types: 1) A border of 1–2 rows of larger cells is present in *C. bispinosus* and *C. subporosus*. The border in *C. bispinosus* is particularly well-defined (Fig. 10: 12), especially under the dissecting microscope. 2) A border of 1–2 rows of smaller cells occurs in *C. monoicus* (Fig. 41: 4) and is of value because it is the only member of sect. *Semiteres* with this feature. 3) In *C. subporosus*, and to a lesser extent *C. bispinosus*, intramarginal cells may consist of mostly small cells, but scattered among them are conspicuously enlarged cells (Fig. 13: 2, *C. subporosus*). No other Australasian members of sect. *Lophocolea* have this character, which is readily observed under the dissecting microscope, the leaves appearing speckled. 4) All species of sect. *Leucophylli* have a median–basal field of cells that is inflated and in sharp contrast to the ± isodiametric distal cells (Fig. 65: 6, *C. leucophyllus*, showing the limits of that field).

Trigones are a useful taxonomic feature. Trigone size and terminology follows Schuster (1966). They are totally lacking in *C. excisifolius*, but for the most part, trigones vary from small to medium or, in other taxa, from medium to large and bulging to knot-like. The knot-like trigones are a subgeneric character for the *Connati*.

Underleaf cell characters usually are not used taxonomically in the Hepaticae, but they are of diagnostic value in the *Leucophylli*. Underleaf cell tuberculae are lacking in *C. connatifolius* but present in all other species of the section. Furthermore, the taxa with tuberculae also have a median–basal field of enlarged underleaf cells (ill-defined in *C. aculeatus*) in contrast to a distal sector of ± isodiametric cells (Fig. 65: 5, *C. leucophyllus*, showing the limits of that field). *Chiloscyphus connatifolius* lacks such isodiametric cells in the underleaf (Fig. 67: 2); the underleaf cells are all inflated similarly to those of the basal leaf cells (Fig. 67: 8).

OIL-BODIES—Oil-body characters in regional *Chiloscyphus* taxa are taxonomically relevant at specific and infraspecific levels. Three oil-body character states have been particularly useful in differentiating taxa.

1) Color/translucency. The vast majority of Australasian *Chiloscyphus* taxa have hyaline oil-bodies. However, a few noteworthy exceptions exist. Among the muricate species, greyish oil-bodies occur in *C. parvispineus* and at least at times in *C. muricatus* (Schuster, 1980). Grey oil-bodies will differentiate these species from *C. villosus*, which has uniformly hyaline oil-bodies. Oil-body differences are useful in distinguishing members of the *C. semiteres*–*C. rupicola* complex. *Chiloscyphus rupicola* has opaque oil-bodies, whereas *C. semiteres* has hyaline oil-bodies. *Chiloscyphus canaliculatus* may be distinguished from the other taxa in the complex by its greyish-orange oil-bodies. (Oil-bodies of *C. semiteres* var. *retusus* are unknown.)
2) Number. Oil-body number per cell is mostly in the range of 2–7; taxa with 1 or 8–12 oil-bodies per cell are exceptional. Oil-body number may be used to separate *C. suboppositus*, which has 3–5 oil-bodies per cell, from its ally *C. edentatus*, which has 2 oil-bodies per cell. The number per cell also may be used to separate *C. novaezeelandiae* (2 or 3) from the allied *C. hattorii* (3–6).
3) Surface characters. Oil-bodies vary from sharply granular to, more often, coarsely papillose to coarsely botryoidal; categories of oil-body surface features follow Engel and Glenny (2008b). Variation within a species sometimes occurs; for example, *C. novaezeelandiae* has finely papillose to coarsely botryoidal oil-bodies. Surface characters are of taxonomic value in differentiating certain species pairs. For example, *C. cuspidatus* has coarsely papillose to finely botryoidal oil-bodies, whereas *C. longiciliatus* has oil-bodies coarsely botryoidal.

UNDERLEAVES—All Australasian *Chiloscyphus* taxa possess wide ventral merophytes that produce conspicuous underleaves.

The absence vs. presence of leaf–underleaf connation (fusion) and the degree of that connation are of considerable taxonomic value. Underleaves may be free or connate on one or both sides with the lateral leaves. They are free in several taxa of sect. *Lophocolea*, and this feature is important in distinguishing these taxa from those that have uniformly connate underleaves. Underleaves are conspicuously connate on both sides in subg. *Connati*.

In some cases it is difficult to establish the presence of connation with certainty with the dissecting microscope. In all such cases of uncertainty, the presence vs. absence of connation must be checked with the compound microscope, preferably with ca. 100× magnification. During the course of these investigations, numerous instances occurred where underleaves were thought to be narrowly connate under the dissecting microscope but were actually distinctly free under the compound scope. Numerous instances of the opposite condition also occurred.

Lateral armature of the underleaf lamina may be absent altogether, as frequently occurs in *C. austrigenus* (Fig. 2: 1, 3–5). A few teeth may be present on the lamina margin, as in *C. novaezeelandiae*, but more often, taxa of *Chiloscyphus* have one process, usually median in position. That process has great variability in magnitude within the genus, varying from a small tooth to a lobe nearly equivalent in size to one of the median lobes (as in well-developed populations of *C. lentus*; Fig. 7: 9). Lobing of the underleaf lamina attains maximum development in *C. spinifer*, a species with 6 well-developed lobes (Fig. 48: 5, 11).

Various underleaf dimensions were calculated. The sinus depth was measured (Fig. 1: 3) by extending a line (b) from the median uppermost point of the line of insertion through the maximum depth of the sinus to the point of intersection with line (a). Line (a) connects the segment tips.

The underleaf width, which is normally used here in reference to comparisons with stem width, was measured by a line connecting the lateral margins at the widest point of the lamina. Because of the high variability in magnitude of lamina armature, the width of the underleaf was restricted to the lamina. However, lamina armature was included in measurements of underleaves with very large, crowded, lateral lobes, which obliterate definition of the lamina (e.g., see Fig. 1: 3, line c).

ASEXUAL REPRODUCTION—Australasian representatives of the genus exhibit three methods of asexual reproduction. 1) Regeneration, which involves the dedifferentiation of an adult leaf cell, which then becomes meristematic and capable of producing a new gametophytic plant through a plantlet phase. This type of reproduction generally occurs on older sectors of shoots. This type occurs in four species of subg. *Lophocolea*—*C. lentus* (Fig. 9: 8), *C. subporosus*, *C. longiciliatus*, and *C. perpusillus* (Fig. 26: 8)—as well as one species, *C. gippslandicus* (Fig. 75: 11, 12), of subg. *Microlophocolea*. Paton (1999, fig. 194) illustrated regenerative buds in *C. semiteres*. 2) Caducous leaf lobe tips occur in *C. perpusillus* and possibly *C. helmsianus*. 3) Gemmae formation is rare among members of *Chiloscyphus* and is of two types depending on origin: a) Gemmae from leaf margins occur in *C. erosus* (Fig. 27: 8) of sect. *Lophocolea* and *C. novaezeelandiae* of sect. *Novarum-zeelandiarum*. They also occur in such examples as the holarctic *C. minor* (Nees) J. J. Engel & R. M. Schust. (see Schuster, 1980, 1997b). b) Gemmae produced from leaf lobe tips are found in *C. perpusillus* (Fig. 26: 5) of sect. *Lophocolea*. As pointed out in Engel (1993), this species has the ability to form gemmae from the juvenile or regenerate state, and, as mentioned by Engel (1993, p. 246), it "does not have a persistent juvenile phase, but is neotenic in its ability to reproduce from that juvenile stage." In this respect it is highly unusual among liverworts. It is notable that all three modes of asexual reproduction are present in *C. perpusillus* (see Engel, 1993).

SEXUALITY—Positive establishment of sexuality is crucial in sect. *Lophocolea* and must be done with great care. Sometimes this involves careful dissection of an entire mat of a specimen, and a lengthy search at times is rewarded by a single shoot exhibiting a physical connection between male and female sectors of the plant. The difficulty of establishment of a physical connection is related to the stage of the plant and relative maturity of sex organs, as well as the frequent decay of that part of the plant that connects male and female (which at times appears to be part of the previous year's growth). Androecia are sometimes very difficult to demonstrate, if a population has perianths less than the height of the bracts or if gynoecia are in a stage before leaf fusion. (In the latter case, gynoecia are recognizable by their enlarged leaves and may be confirmed by checking for presence of archegonia.) For example, *Engel 13023* of *C. cuspidatus* has young gynoecia and androecia not readily apparent, but a lengthy, careful search revealed a clearly monoecious plant. Norris 30230 (F) also will serve to illustrate some of the difficulties; that plant consists of some shoots with androecia and others with gynoecia in the pre– or early leaf fusion stages and, in addition, old, partially decayed shoots with gynoecia from the previous year. Approximately 50 shoots had to be examined carefully before one could be found to demonstrate clear bisexuality. In this case, a shoot was found with gynoecia in the pre–leaf fusion stage and was identifiable as female only by presence of archegonia and slight swelling of shoot tip. Vegetative characters were used to confirm identity. In general, the younger the gynoecium, the greater the difficulty of locating androecia. Fertilization does not appear to occur when gynoecia are in the pre–leaf fusion state or if perianths are less than the bract height. It appears that when gynoecia have reached such a stage of perianth development, the archegonia are fully mature and androecia are then synchronously formed on the same plants, and fertilization would occur subsequent to this stage. This synchronous production of mature archegonia and antheridia would appear to be a mechanism to enhance fertilization by gametes from the same plant or same clone, thereby increasing spore production.

Plants with young androecia may also present problems for establishing sexuality. Here male bracts have an incomplete lobule, the margin merely being sharply oriented toward the shoot apex and only suggestively saccate. In such cases, searching for perianths from the previous year may reveal a physical connection between sexes (e.g., *Engel 19382* of *C. longiciliatus*).

Large plants with piliferous leaf segments, large leaf cells, free underleaves that are bifid nearly to the base and an underleaf disc with a prominent lacinium should be suspected as autoecious, in that all of these vegetative features are of the *C. cuspidatus* complex. However, care and patience in search of fertile shoots are required to confirm or reject that condition and thereby that complex. Fortunately, members of the *C. cuspidatus* complex are often fertile, permitting that confirmation.

ANDROECIA—Androecia occur on a variety of branch types within *Chiloscyphus*. Table 1, placed below under "gynoecia," surveys androecial vs. vegetative branch types with Australasian species of the genus. A number of species have differences between vegetative and androecial branch types. In nearly all cases, these differences involve fewer androecial branch types compared with vegetative branching modes.

It is useful to distinguish the androecium found in *Chiloscyphus* with that in *Heteroscyphus*. The latter genus is defined in part by the possession of spicate androecia positioned on abbreviated, leafless, lateral-intercalary branches (i.e., the heteroscyphoid type).

Several species of *Chiloscyphus* have spicate androecia that occur on short lateral-intercalary branches, and these taxa are useful in assessment of the taxonomic value of the heteroscyphoid androecial character in that genus. *Chiloscyphus helmsianus* may be cited as an example. In that species, heteroscyphoid androecia represent an extreme in a continuum of the androecial branch character state. That extreme is characterized by short, determinate, spicate androecial branches that do not exceed the length of the leaf immediately above. Such branches often are located on the same shoot as, and often distal to, branches that are longer, indeterminate, and have subfolious (chiloscyphoid) androecia. Figure 51 (sector 4) shows the difference in magnitude of two heteroscyphoid androecia a few gyres apart. Both spicate and subfolious androecial branches of *C. helmsianus* frequently proliferate vegetatively distally, resulting in androecia that are then basal on a branch. Such branches may, in turn, produce terminal androecia that again may become intercalary. Furthermore, androecial branches often are accompanied by androecia that are terminal or intercalary in position on the main shoot (Fig. 51: 2).

The spectrum of variation in *C. helmsianus* outlined above is similar to that found in other Australasian species of the genus possessing spicate ± heteroscyphoid androecia. The heteroscyphoid condition is not fixed within the genus, and species that have such male branches also possess androecia on main shoots as well as elongate branches. On the other hand, the determinate, abbreviated, spicate androecial character state in *Heteroscyphus* is fixed and consequently is of taxonomic value at the generic level. Androecia in *Heteroscyphus* are lacking on both the main shoot and the elongate branches; furthermore, androecial branches are never indeterminate or subfolious.

Androecia in regional *Chiloscyphus* vary from distinctly foliose to distinctly spicate. Distinctly foliose androecia occur in *C. herzogii*, where we find bracts remarkably leaf-like in size and form except for the presence of a dorsal pocket (Fig. 20: 4). Androecia with such characteristics vary toward the subfolious condition (Fig. 62: 11, *C. aculeatus*; Fig. 48: 1, *C. spinifer*) to the subspicate state. Spicate androecia are much narrower than vegetative shoot sectors and have bracts strongly differentiated in size and form from the leaves (Fig. 54: 12, *C. multipennus*; Fig. 57: 7, *C. trialatus*). Here we find bracts that are strongly ventricose-subcucullate, and the dorsal pocket is large in proportion to the bracts.

Lobules of regional *Chiloscyphus* are incurved to involute and possess some armature. The lobule margin varies from sparingly to copiously crenulate to crenate-dentate to dentate-ciliate to, less often, ciliate-laciniate (Fig. 62: 6, *C. aculeatus*). Additionally, a distal process is commonly also present and varies from dentiform to laciniiform (Fig. 54: 13, *C. multipennus*). The margin occasionally has only a distal process and otherwise lacks other armature, as in *C. suboppositus*.

Androecial paraphyses occur in only one regional species, *C. helmsianus* (Fig. 51: 6, 7). They occur at the base of the inner or outer face of the lobule near the juncture of lobule and stem. They are otherwise rare in the family.

Laterally fused androecial bracts are present in all except five species of *Chiloscyphus*. *Clasmatocolea*, on the other hand, has fused bracts in only three species, the remainder of taxa having free bracts (Engel, 1980). Fused bracts in *Clasmatocolea* occur in the primitive subg. *Lacerifolia* (two species) and again in *C. minutretis*, a derivative species of subg. *Clasmatocolea*. Free bracts occur in the primitive *C. austrigenus*, and again in three derivative species: *C. monoicus*, *C. mittenianus*, and *C. muricatus*.

Antheridia are solitary and only rarely occur two or three per bract. Antheridial stalks proved to be a valuable character at the subgeneric level. Stalks are biseriate in subg. *Connati* and uniseriate in regional taxa of all other subgenera except subg. *Septati*. The last is very unusual among Hepaticae in having multiseriate antheridial stalks (Fig. 47: 5).

GYNOECIA—Gynoecia in regional *Chiloscyphus* taxa are found on the main shoot (in all species), as well as the three branch types mentioned above under branching. However, a number of species have differences between vegetative and gynoecial branch types, and the pattern of these differences is similar to androecial branch types discussed above. In nearly all cases, these differences involve fewer gynoecial branch types compared with vegetative branching modes. Exceptions occur in sect. *Semiteres*, wherein gynoecia are borne on branch types not represented vegetatively (see Table 1). Interestingly, two of our species have complete loss of gynoecial branches; in *C. calcareus* (subg. *Lophocolea*) and *C. mittenianus* (subg. *Connati*), gynoecia are restricted to the main shoot and never occur on branches. In *C. aperticaulis*, gynoecia are restricted to the main shoot and subfloral innovations.

Ventral-intercalary gynoecial branches occur in all subgenera except subg. *Connati*, which also lack ventral-intercalary vegetative branches.

Several subgenera have taxa with gynoecial branches of variable length, some branches with few to many vegetative leaves, and others completely lacking them; examples of such involve all three branch types. Gynoecia on leafless lateral shoots frequently occur in sect. *Semiteres*, for example, and this condition is of significance in evaluation of the taxonomic position of *Chiloscyphus* in the strict sense (see Engel and Schuster, 1985).

BRACTS—Bract form does not deviate to any major extent from that of the leaves. Those taxa with bifid leaves also have bifid bracts, whereas those with undivided leaves also have undivided bracts. But bracts occasionally deviate in form from leaves, especially in the muricate species. *Chiloscyphus parvispineus* has leaves with armature restricted to the dorsal surface but has bracts with both dorsal and ventral surfaces armed. *Chiloscyphus gippslandicus*, on the other hand, has leaves frequently armed with surface teeth but has bracts (and perianths) completely smooth. *Chiloscyphus calcareus* has fundamentally undivided leaves (although they may be retuse-bilobed), but may have distinctly bifid bracts.

Although bracts increase in size toward the perianth, the bract sinus depth in bifid-leaved taxa is similar to that of leaves. Leaf-bract similarity also may be found in several of the taxa with leaves that vary from undivided to bifid (e.g., *C. rupicola*, *C. gippslandicus*), where bract apices have similar plasticity.

BRACTEOLES—Moderate anisophylly to isophylly is achieved in at least some members of all Australasian sections of *Chiloscyphus*, except in all species of subg. *Microlophocolea*. Exceptionally small bracteoles for the genus are found in this group, e.g., *C. muricatus* has bracteoles 0.35 the bract size and *C. parvispineus* ca. 0.4 the bract size.

Connation patterns of the bracteoles (free compared with connate on one or both sides), in general, are similar to those of leaves. Bracteole connation, however, tends to be somewhat broader than underleaf connation.

PERIANTHS—The trigonous, "Epigoniantheae"-type perianth has been regarded to have arisen from a terete perianth

TABLE 1. Vegetative compared with sexual branch types of Australasian *Chiloscyphus*. Table identifies the species in which sexual and vegetative branch types differ. Types that occur vegetatively but do not bear gynoecia or androecia are shown with a minus sign [−] in the appropriate column. Those branch types that bear gynoecia or androecia but do not occur vegetatively are shown with a plus sign [+] in the appropriate column. F = *Frullania*-type branch; LI = lateral-intercalary branch; V = ventral-intercalary branch.

Taxon	Vegetative branch types	Gynoecial differences	Androecial differences
Subg. *Notholophocolea*			
Sect. *Notholophocolea*			
C. austrigenus	F, LI, VI	−F	−LI
Subg. *Lophocolea*			
Sect. *Lophocolea*			
C. lentus	F, LI, VI	−F, −VI	−VI
C. bispinosus	F, LI, VI	−F	−F
C. longiciliatus	F, LI, VI		−VI
C. excisifolius	F, LI		−F
C. perpusillus	F, LI	−F	+ VI
C. erosus	F, LI, VI	−F	
Sect. *Novarum-zeelandiarum*			
C. novaezeelandiae	F, LI	−F	−F
C. calcareus	F, LI	−F, −LI	−LI
Sect. *Semiteres*			
C. semiteres	F, LI	+ VI	
C. fertilis	LI	+ F	
Sect. *Aperticaules*			
C. aperticaulis	F, LI	−F, −LI	−F
Subg. *Septati*			
C. septatus	LI, VI	−?	−LI
Subg. *Connati*			
Sect. *Spiniferi*			
C. spinifer	F, LI	−LI	−LI
Sect. *Connati*			
C. edentatus	F, LI		−LI
C. suboppositus	F, LI	−F	−F
C. trialatus	F, LI	−F	
Sect. *Leucophylli*			
C. aculeatus	F, LI	−F	−F
C. mittenianus	F, LI	−F, −LI	
Subg. *Microlophocolea*			
Sect. *Hemispini*			
C. parvispineus	F, LI	−F	
C. gippslandicus	F, LI	−F	−F
Sect. *Microlophocolea*			
C. villosus	F, LI, VI	−F, −VI	
C. muricatus	F, VI	−F	

or "urn-shaped cup" (see Fulford, 1965; Schuster, 1966, including fig. 52). All regional species of *Chiloscyphus*, with one exception, have a sharply trigonous perianth, at least in the distal half. The primitive condition in *Chiloscyphus* is characterized by a sharply trigonous perianth with each of the three lobes at least shortly bifid, reflecting the nature of the foliar structures from which they originated. Furthermore, the points of fusion of the leaves are frequently delineated by the presence of wings (see below), which are not only a remnant, but a reminder of the origin of the perianth from leaves. *Chiloscyphus muricatus* is the only regional species of the genus with a terete perianth (Schuster, 1980, fig. 531: 3); that species belongs to a highly derivative subgenus, *Microlophocolea*. *Chiloscyphus anisolobus* has terete perianths, but with maturity, the perianths become somewhat bilaterally compressed (Fig. 24: 7).

Trigonous perianths have the three faces equal in width, or nearly so, but deviations occur toward a slightly narrower ventral lobe. That slight narrowing occurs in several taxa, such as *C. novaezeelandiae* (Fig. 30: 5), *C. multipennus* (Fig. 54: 5), and *C. leucophyllus* (Fig. 66: 7). Substantial reduction of the ventral lobe occurs in *Clasmatocolea*, frequently in taxa of that genus with terete perianths (Engel, 1980). That correlation is lacking in Australasian *Chiloscyphus* taxa, wherein *C. muricatus* has a nearly perfectly terete perianth that is ± equally three-lobed at the mouth (Fig. 79: 5).

Most species have all three of the perianth lobes bifid. The lobes are usually deeply bifid in taxa with fundamentally bilobed leaves (Fig. 7: 5, *C. lentus*) and less deeply divided in taxa with undivided leaf apices (Fig. 32: 9, *C. hattorii*; Fig. 36: 6, *C. semiteres*). Variation involving the leaf apex at times also may be similarly found in the perianth lobes. For example, both leaves and perianth lobes of *C. rupicola* are undivided to short bifid. Not all taxa with bilobed leaves have bifid perianth lobes (*C. leucophyllus*, e.g., has undivided perianth lobes; Fig. 66: 7). The reverse of this condition occurs in *C. austrigenus*, in which leaves are uniformly undivided, but perianth lobes are retuse-bidentate to short bifid (Fig. 3: 1, 3). *Chiloscyphus* fertilis is the only species to have both undivided leaves and (usually) undivided perianth lobes (Fig. 38: 4, 11).

I have used the term "keel" in relation to the perianth to refer to the suture or line of fusion of two lobe faces. The term as I use it thus has a broader meaning than Stearn (1998, p. 313), who defines "carinatus" or "keeled" as "formed in the manner of the keel of a boat ... with a sharp projecting ridge arising from a flat or concave central rib." Some species have perianths that have these characters in the strict sense (i.e., a cluster of cells projecting outward from the suture). However, most species do not have a demonstrable rib (apart from the "wing," cf. below) at the juncture of two perianth lobes. With the use of the term in the broad sense, in sharply trigonous perianths the keel is well-defined (Fig. 3: 1, 10, *C. austrigenus*). The term "keel" becomes less applicable with increased inflation toward the terete perianth condition; it has little relevance to terete perianths.

I have used "wing" to indicate lamella-like flaps of tissue projecting from the keel or suture. They may be variously armed and are inconspicuous and of a few cells high to obvious, of many cells high and at times undulate. Wings are present and often common in most species but lacking or sporadic in the derivative section *Semiteres*. Wings are particularly well-developed in sect. *Connati*, in which they are exceptionally high, often undulate and present on all three keels (Fig. 58: 6, 8, *C. trialatus*).

SETA—The seta for the most part exhibits no sharp internal differentiation. The cells of the epidermal layer are smaller than, equal to, or larger than the internal cells. The derivative *C. muricatus*, however, has sharply delimited epidermal cells that surround relatively few (9) much smaller internal cells (Fig. 79: 12). The number of cells in the epidermal row is rather low and varies from 10 in *C. muricatus* (Fig. 79: 12) to 36 in *C. spinifer* (Fig. 49: 4). The number of cells in seta diameter also varies (5 in *C. muricatus* to 11 in *C. spinifer*).

CAPSULE—Capsule shape is mostly ellipsoid or, in a few species, ellipsoid to obovoid or ellipsoid to wide ovoid. A clear exception is *C. trialatus*, which has long-ellipsoid to cylindrical capsules (Fig. 56: 8). Capsule tips are rounded and never acute or beaked.

Capsule walls are 4–6-layered, with two species at least at times having fewer than 4 layers. In *C. muricatus* it is 2–3-

stratose (Fig. 79: 6, 7) and in *C. lentus* 3–4-stratose. The outer wall is always thicker, equivalent to at least 1.5–3.5 of the interior strata. Several taxa have the outer layer equal to or exceeding the thickness of all interior strata. The outer layer has strictly nodule-like or nodule-like to spine-like thickenings that are mostly on the longitudinal radial walls and, less frequent, sporadic or lacking on transverse walls. Semiannular bands are lacking in most species and sporadic in a few. This condition differs from *Clasmatocolea*, which has semiannular bands in the epidermal cells of all except two species. Several species (four in subg. *Lophocolea*, one in subg. *Connati*) have a weak tendency toward the two-phase type of distribution of thickenings in epidermal cells. These species have longitudinal walls with rather dense thickenings alternating with those with few or no thickenings. The intermediate layers of the capsule wall are rather uniform in wall features and possess thickenings on radial walls that are tangentially dilated. The intermediate and inner layers are subequal in thickness. The inner layer of cells has semiannular bands extending from radial onto tangential walls. The radial walls often have nodular or spine-like thickenings interspersed with the bands. The bands may fork and anastomose to delimit fenestrae. The fenestrae are common but not universal in subg. *Connati*—they occur in all species of sect. *Leucophylli* (Fig. 70: 13, *C. mittenianus*), sect. *Spiniferi* (in which they are rather ill defined in *C. spinifer*; Fig. 49: 2), and several species of sect. *Connati* (Fig. 56: 3, *C. suboppositus*). Fenestrate thickenings are lacking in all other regional *Chiloscyphus* taxa except *C. perpusillus* (subg. *Lophocolea*).

Spores—The spore wall in regional *Chiloscyphus* is markedly uniform, and nearly all species have dense, low, close papillae and short vermiculate markings. The single exception to the pattern of wall sculpture is *C. gippslandicus*, which has a network of wide, irregular coalescing vermiform ridges. This rather uniform wall sculpture is in contrast to *Clasmatocolea*, which has two very different spore types. One type is similar to the walls of Australasian *Chiloscyphus*, and the other has elongate projections. The latter type is restricted to corticolous taxa, and presence appears to correlate with ecology. That type is not represented in our species of *Chiloscyphus*, perhaps because of the lack of strictly corticolous Australasian species.

The spore:elater diameter ratio varies within rather narrow boundaries, being 1.1–2.1:1—*C. trialatus* being the only exception. The ratio in that species is 0.85–1:1. Most species have spores in the 9–15 µm range; the smallest spores are 8.2–9.6 µm in *C. multipennus*, and the largest are 13.9–16.8 µm in *C. novaezeelandiae*. The large spores of *C. novaezeelandiae* distinguish that species from its ally, *C. hattorii*, which has smaller spores (10.1–11.5 µm).

Elaters—Regional species of *Chiloscyphus* have bispiral elaters that taper gradually toward the ends. Elaters are 6–11 µm in diam., with spirals 1.9–3.4 µm wide. Elaters are uniformly unbranched, except in *C. suboppositus*, in which they often branch (Fig. 56: 6).

For terminology and abbreviations, I follow Stearn (1998) and the glossary found in Engel and Glenny (2008b).

Conspectus of Australasian Taxa of *Chiloscyphus*

- subg. *Notholophocolea* (R. M. Schust.) J. J. Engel & R. M. Schust. (p. 12)
  - sect. *Notholophocolea* J. J. Engel (p. 12)
    - *C. austrigenus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust. (p. 12)
      - [subsp. *austrigenus*] (p. 16)
      - subsp. *okaritanus* (Steph.) J. J. Engel (p. 16)
- subg. *Lophocolea* (Dumort.) J. J. Engel & R. M. Schust. (p. 20)
  - sect. *Lophocolea* (Dumort) J. Hentschel (p. 20)
    - *C. lentus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust. (p. 23)
    - *C. bispinosus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust. (p. 31)
    - *C. subporosus* (Mitt.) J. J. Engel & R. M. Schust. (p. 40)
      - var. *subporosus* (p. 45)
      - var. *inflexifolius* (Steph.) J. J. Engel (p. 49)
    - *C. cuspidatus* (Nees) J. J. Engel & R. M. Schust. (p. 50)
    - *C. longiciliatus* (Herzog) J. J. Engel & R. M. Schust. (p. 56)
    - *C. herzogii* J. J. Engel & R. M. Schust. (p. 59)
    - *C. excisifolius* (Steph.) J. J. Engel & R. M. Schust. (p. 61)
    - *C. anisolobus* J. J. Engel & Glenny (p. 63)
    - *C. perpusillus* (Hook. f. & Taylor) J. J. Engel (p. 67)
    - *C. erosus* J. J. Engel (p. 72)
  - sect. *Novarum-zeelandiarum* J. J. Engel (p. 74)
    - *C. novaezeelandiae* (Lehm. & Lindenb.) J. J. Engel & R. M. Schust. (p. 75)
      - var. *novaezeelandiae* (p. 80)
      - var. *meridionalis* (Steph.) J. J. Engel (p. 82)
      - var. *grandistipulus* (Schiffn.) J. J. Engel (p. 83)
    - *C. hattorii* J. J. Engel (p. 84)
    - *C. calcareus* (Steph.) J. J. Engel & R. M. Schust. (p. 87)
  - sect. *Semiteres* J. J. Engel (p. 90)
    - *C. semiteres* (Lehm.) Lehm. & Lindenb. (p. 91)
      - var. *semiteres* (p. 97)
      - var. *retusus* J. J. Engel, var. nov. (p. 103)
    - *C. canaliculatus* Gottsche, Lindenb. & Nees (p. 103)

var. *canaliculatus* Gottsche, Lindenb. & Nees (p. 106)
var. *concavus* J. J. Engel, var. nov. (p. 107)
C. fertilus J. J. Engel (p. 107)
C. rupicola (Steph.) J. J. Engel & R. M. Schust. (p. 110)
C. monoicus J. J. Engel & R. M. Schust. (p. 115)
sect. *Aperticaules* J. J. Engel, sect. nov. (p. 119)
C. mediinfrons J. J. Engel & Braggins, sp. nov. (p. 119)
C. aperticaulis J. J. Engel (p. 120)
subg. *Septati* J. J. Engel, subg. nov. (p. 125)
C. septatus J. J. Engel, sp. nov. (p. 125)
subg. *Connati* (Lindenb.) J. J. Engel (p. 127)
sect. *Spiniferi* J. J. Engel (p. 128)
C. spinifer (Hook. f. & Taylor) J. J. Engel & R. M. Schust. (p. 128)
sect. *Connati* (Lindenb.) J. J. Engel, comb. nov. (p. 133)
C. helmsianus (Steph.) J. J. Engel & R. M. Schust. (p. 134)
C. multipennus (Hook. f. & Taylor) J. J. Engel & R. M. Schust. (p. 137)
C. suboppositus J. J. Engel (p. 143)
C. trialatus (Gottsche) J. J. Engel & R. M. Schust. (p. 147)
C. edentatus J. J. Engel (p. 152)
sect. *Leucophylli* J. J. Engel (p. 154)
C. tuberculatus J. J. Engel (p. 156)
C. aculeatus Mitt. (p. 161)
C. leucophyllus (Hook. f. & Taylor) Gottsche, Lindenb. & Nees (p. 163)
C. connatifolius J. J. Engel (p. 170)
C. mittenianus (Colenso) J. J. Engel (p. 173)
var. *mittenianus* (p. 175)
var. *obtusus* J. J. Engel (p. 179)
var. *symmetricus* J. J. Engel (p. 179)
subg. *Microlophocolea* (Spruce) J. J. Engel (p. 181)
sect. *Hemispini* J. J. Engel (p. 181)
C. parvispineus J. J. Engel (p. 182)
C. gippslandicus J. J. Engel & R. M. Schust. (p. 187)
sect. *Microlophocolea* (Spruce) J. J. Engel & R. M. Schust. (p. 190)
C. villosus (Mitt. ex Steph.) J. J. Engel & R. M. Schust. (p. 190)
C. muricatus (Lehm.) J. J. Engel & R. M. Schust. (p. 196)
subg. *Spinoscyphus* J. J. Engel. subg. nov. (p. 199)
C. trichcocoleoides Glenny, J. J. Engel & He-Nygrén (p. 199)

Chiloscyphus **Corda**

Chiloscyphus Corda *in* Opiz (ed.), Beiträge zur Naturg. (12): 651. 1829 ("*Cheilocyphos*"); corr. Dumortier, Sylloge Jungerm. Europ. Indig. 67. 1831, nom. et orth. cons. Type: *Chiloscyphus polyanthos* (L.) Corda.

Jungermannia sect. *Lophocolea* Dumort., Sylloge Jungerm. Europ. Indig. 59. 1831. *Lophocolea* (Dumort.) Dumort., Recueil Observ. Jungerm. 17. 1835. *Chiloscyphus* sect. *Lophocolea* (Dumort) J. Hentschel, Pl. Syst. Evol. 262: 129. 2006. Type: *Jungermannia bidentata* L.

Gamochaetium Trevis., Memorie Real. Istit. Lombardo Sci. Mat. Nat. Ser. 3, 4: 397. 1877. Type: *G. concretum* (Mont.) Trevis. ≡ *Lophocolea concreta* Mont.

Plants prostrate to erect, various shades of green and, less frequently, brown, the main shoots of smaller species to 0.8 mm wide, of larger species to 5 mm wide. Branching variable, the branches of lateral-intercalary and *Frullania* types, both common; ventral-intercalary branches occasional; stolons absent. Stems with cortex in 1–2 rows or with cortex hardly differentiated. Paraphyllia typically lacking, present in *C. trichocoleoides* and ventrally in *C. villosus*. Rhizoids colorless, from stem at base of underleaf, rarely becoming scattered (*C. multipennus*), the tips simple or branched, rarely septate (*C. septatus*). Leaves alternate to subopposite to opposite, connate or free dorsally, the orientation mostly strongly succubous, occasionally subtransverse, the insertion strongly succubous, not or slightly to distinctly recurved at ventral end, the leaves unistratose, mostly convex, occasionally concave but never conchiform concave; apex undivided or fundamentally bifid; margins entire or variously armed with teeth, cilia, or laciniae. Surface of leaves smooth or, in some taxa, tuberculate or hispid. Leaf cells with walls thin, trigones variable, minute to medium to distinctly knot-like. Oil-bodies (1)2–7(12) per cell, mostly coarsely papillose to coarsely botryoidal, occasionally sharply granular. Underleaves distinct, persistent, 0.7–3.7× stem width, free or connate on 1 or both sides, at times broadly so, the insertion crescent to inverted U-shaped, never straight; the underleaves plane to convex or concave, with apices mostly 2(4–6)-lobed to at least 0.4, at times undivided and entire or bidentate or retuse to bifid to 0.3, the lobes, when present, commonly acuminate to subcaudate and with margins entire or variously armed with teeth, cilia, or laciniae; lamina margins entire or dentate to laciniate to lobate.

Asexual reproduction by caducous leaf lobes, regeneration or gemmae that are not produced in fascicles.

Plants dioecious, autoecious, or paroecious; androecia terminal or intercalary in position on main shoot or, if on short, abbreviated branches, then never consistently so; bracts similar in size to vegetative leaves grading to much smaller, usually fused toward base with opposite bract, the dorsal base dilated and forming an infolded flap or lobule; lobule margin commonly with a distal process and, often, sparingly to densely armed with teeth and cilia; antheridia solitary, rarely 2–3 per bract, the stalk 1–2-seriate; paraphyses rare. ♂ Bracteoles without antheridia. Gynoecia on main shoot or elongated branches or short, abbreviated lateral- or ventral-intercalary branches, rarely on short, abbreviated *Frullania*-type branches. Vestigial stem perigynium often present, sometimes fleshy and 7–9 cells thick near base, with 1–2 or 3–4 pairs of bracts inserted on the perigynium. Bracts of innermost series with apices undivided to retuse or bifid; margins entire or dentate to ciliate to laciniate. Bracteoles of innermost series conspicuous, mostly 0.5–1× bract area, occasionally 0.2–0.4× bract area, free or connate on 1 or both sides, sometimes broadly so; apices undivided and entire or bidentate or retuse or 2–4-fid to 0.1–0.7; lamina margins entire or dentate-laciniate-lobate. Perianth elamellate, mostly sharply trigonous, rarely terete, the mouth 3-lobed, the lobes ± subequal or the ventral slightly narrower, the lobes undivided and dentate to laciniate or entire or shallowly to deeply bifid; keels often winged.

Seta in transverse section with epidermal cells not greatly differentiated from the scattered, mostly numerous inner cells. Capsule mostly elliptic, rarely long elliptic to linear, of (2–3)4–6 layers, the outer layer of cells thicker, equal to thickness of at least 1.5–3.5 of interior strata or equal to or exceeding the thickness of all interior strata combined, the outer layer of cells with thickenings mostly on longitudinal radial walls and less frequent or lacking on transverse walls, the thickenings nodule-like to spine-like, semiannular bands at most sporadic; intermediate layers with thickenings on radial walls; innermost layer of cells with thickenings on radial and tangential walls; semiannular bands extending from radial walls, the bands sometimes incomplete, sometimes forked and anastomosing to delimit a series of well-defined fenestrae, the radial walls often with nodule-like to spine-like thickenings.

Spores with dense, low, close papillae and short-vermiculate markings, the spores averaging (0.85)1.1–2.1× elater diameter. Elaters bispiral.

The Genus *Chiloscyphus* in Australasia

Synoptic Key to Australasian Subgenera and Sections of *Chiloscyphus*

1. Dorsal (and sometimes ventral) leaf surfaces armed with conspicuous sharp-pointed laminar and marginal processes formed of 1 to several cell; perianths armed on external (and often internal) surfaces with spinose cellular processes. Antheridial stalk 1-seriate 2

  2. Leaf insertion extending to stem midline dorsally; gynoecia variable in position: acrogynous or cladogynous (the cladogynous lateral- or ventral-intercalary, often or usually bearing vegetative leaves). Capsule wall surface unarmed. Auto- or dioecious. subg. *Microlophocolea* 3

    3. Ventral surface of leaf (suboptimal plants aside) with teeth; underleaf segments with opposing teeth or cilia, the abaxial surface of both segments and lamina often with scattered teeth; ventral-intercalary branches at least sometimes present. Autoecious or dioecious . . . . sect. *Microlophocolea* (p. 190)

    3. Ventral surface of leaf uniformly smooth; underleaf segments entire or at most with 1–2 teeth, the teeth never regularly opposing, the abaxial surface of both segments and lamina smooth; ventral-intercalary branches lacking. Dioecious . . . . sect. *Hemispini* (p. 181)

  2. Leaf insertion not extending to stem midline dorsally and delimiting a broad leaf-free gutter 6–10 cells wide; gynoecia usually on abbreviated ventral-intercalary branches devoid of vegetative leaves. Capsule wall surface with a network of hyaline ridges. Dioecious . . . . [*Cyanolophocolea echinella*] (p. 203)

1. Leaf surfaces smooth or armed with thick-walled tubercles; perianths smooth, never armed with spinous processes. Antheridial stalk 1- or 2-seriate 4

  4. Aspect heteroscyphoid: subopposed leaves consistently and distinctly connate with adjacent, large, conspicuous and broad underleaves, thus each gyre bearing a single, continuous, leaf complex; antheridial stalks biseriate; innermost capsule wall cells with semiannular bands often furcate and anastomosing to delimit fenestrae. Trigones consistently knot-like but with conspicuous thin intervening walls (exc. in *Spiniferi*). subg. *Connati* 5

    5. Leaf, underleaf (exc. *C. connatifolius*) and perianth cells armed on both surfaces with prominent, central, dome-like, thick-walled tuberculae, one per cell (or if tuberculae obscure or appearing absent (*C. aculeatus*), then with leaf segments subcaudate to piliferous and underleaves 4-lobed, divided to 0.5 or less and with disc high) . . . . sect. *Leucophylli* (p. 154)

    5. Leaf and underleaf cells smooth, without protuberances of any sort[1] 6

      6. Underleaves 2–4-lobed or -lobulate, very broadly connate with lateral leaves, without conspicuous basal teeth; leaf cells with nodose trigones; leaf apices often unequally bilobed: the ventral lobe larger than the dorsal. . . . . sect. *Connati* (p. 133)

      6. Underleaves asteroid, (4–)6-lobed and with basal accessory teeth, narrowly connate with lateral leaves; leaf cells with small trigones; leaf apices subequally bilobed . . . . sect. *Spiniferi* (p. 128)

  4. Aspect chiloscyphoid: leaves usually clearly alternate, never conspicuously united with underleaves to form solitary ring-like units, one per gyre, the underleaves free or narrowly connate with leaves on one side (or if consistently narrowly connate on both sides, then connation obscure); antheridial stalks 1-seriate (biseriate in *Lamellocolea*); innermost capsule wall cells with complete to incomplete to spur-like tangential thickenings that fail to fork or fork only sporadically and do not delimit fenestrae (exc. *C. perpusillus*) 7

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[1] It must be established with certainty that tuberculae are absent; see notes under sect. *Leucophylli* (p. 155).

7. Perianth with longitudinal lamellae, even when young; innermost bracteole reduced, only 0.1–0.2 the bract size; antheridial stalks biseriate; outer capsule wall cells with sparingly developed peg-like, mostly hyaline thickenings . . . . . . [*Lamellocolea* J. J. Engel, cf. Engel, 1991c]

7. Perianth surface smooth; innermost bracteole large and conspicuous, at least 0.5 the bract size; antheridial stalks uniseriate (at most with local biseriate areas); outer capsule wall cells with numerous nodule-like, pigmented thickenings 8

8. Leaves with accessory lobes and appearing 4–5-fid, each lobe with primary, secondary, and tertiary toothing; stem paraphyllia well developed, often multiple-branched . . . . . . subg. *Spinoscyphus* (p. 199)

8. Leaves undivided or if divided, then at most 2(3)-lobed; stem paraphyllia lacking (exc. *C. villosus*) 9

9. Ventral-intercalary branching common 10

10. Septate rhizoids present; terminal branching rare; leaves oriented strongly succubous, the insertion slightly recurved at ventral end; antheridial stalk irregularly multiseriate (6-seriate, ?always) . . . . . . subg. *Septati* (p. 125)

10. Septate rhizoids absent; terminal branching present; leaves oriented subtransverse to subsuccubous, the insertion strongly recurved at ventral end, distinctly J-shaped; antheridial stalk 1-, 2-, or 4-seriate . . . . . . subg. *Notholophocolea* (p. 12)

9. Ventral-intercalary branching rare or lacking (exc. *C. erosus*). Leaf orientation strongly succubous, the insertion not or hardly recurved at ventral end, at most weakly J-shaped (exc. sometimes in *C. aperticaulis*). subg. *Lophocolea* 11

11. Leaves fundamentally bilobed . . . . . . sect. *Lophocolea* (p. 20)

11. Leaves fundamentally undivided,[2] the apices on a single shoot at times variable and then rounded to 1- to 2-lobed, but never consistently bilobed (or if uniformly bifid [*C. novaezeelandiae* var. *grandistipulus*] then underleaves concave and divided to 0.4–0.6). (See also separate key to taxa with fundamentally undivided leaves.) 12

12. Leaf insertions not extending to stem midline dorsally, a leaf-free gutter of stem cells present; leaf cell trigones typically completely lacking, at most minute (at times medium to indistinctly bulging in *C. mediinfrons*) . . . . . . sect. *Aperticaules* (p. 119)

12. Leaf insertions extending to stem midline dorsally, a leaf-free gutter of stem cells absent; leaf cell trigones medium and straight sided, rarely minute, never completely lacking 13

13. Gynoecial position variable: some to many on short, lateral-intercalary branches lacking normal leaves (others on leading shoots), at times on terminal branches; leaf apices broadly rounded to retuse or (*C. rupicola*) occasionally short bifid, not polymorphic, the shoots without a combination of undivided, 1- and 2-lobed leaves; perianth wings sporadic or lacking; inner layer of capsule wall cells with radial walls devoid of continuous sheets of pigmented thickening; seta 8–11 cells in diam., with 26–30 epidermal cell rows; gemmae lacking . . . . . . sect. *Semiteres* (p. 90)

13. Gynoecia on main shoots or long leafy branches, never on short intercalary branches that lack vegetative leaves, never on terminal branches; leaf apices often polymorphic, the shoots with a combination of undivided, 1- and 2-lobed leaves; perianth wings rather common; inner layer of capsule wall cells with continuous sheets of pigmented thickening on vertical radial walls; seta (where known) 6–8 cells in diam., with 17–21 epidermal cell rows; gemmae frequent (*C. novaezeelandiae*) . . . . . . sect. *Novarum-zeelandiarum* (p. 74)

Key to Nonhispid Taxa with Fundamentally Undivided Leaves

1. Underleaves undivided and entire or at most bifid to 0.3, the lamina margins at most with 1 process no larger than a tooth; ventral-intercalary branches common . . . . . . *C. austrigenus* (p. 12)

1. Underleaves bifid to 0.4 or more, the lamina margins often with a cilium, lacinia, or lobule or with 2–3 teeth; ventral-intercalary branches lacking (exc. *C. villosus*) 2

2. Leaf insertions not extending to stem midline dorsally, a leaf-free gutter of stem cells present 3

3. Leaf apices uniformly undivided, broadly rounded to truncate to weakly retuse; median leaf cells 18–24 µm wide × 20–32(38) µm long . . . . . . *C. aperticaulis* (p. 120)

3. Leaf apices variable, undivided and 1-dentate to shallowly bifid, occasionally undivided and completely entire; median leaf cells subisodiametric, 36–42 µm wide × 35–46 µm long . . . . . . *C. mediinfrons* (p. 119)

2. Leaf insertions extending to stem midline dorsally, a leaf-free strip of stem cells lacking 4

4. Rhizoids both septate and nonseptate; antheridial stalk multiseptate. Branching nearly exclusively intercalary . . . . . . *C. septatus* (p. 125)

4. Rhizoids all nonseptate; antheridial stalk 1- or 2-septate 5

5. Plants paroecious; leaves with a border of smaller cells . . . . . . *C. monoicus* (p. 115)

5. Plants dioecious; leaves with a border of larger cells or a border lacking 6

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[2] See also separate key to taxa with fundamentally undivided leaves, below on this page.

6. Underleaf discs all or mostly concave (ventral view) 7

7. Underleaf disc margin on each side with 1–2 laciniiform processes and smaller accessory armature; gemmae uniformly lacking 8

8. Cells of leaf middle 22–29 µm wide × 25–31 µm long, with trigones medium to large and bulging; stem with a few paraphyllia ventrally; ventral margin of leaf occasionally with 1 or more teeth . . . . [suboptimal *C. villosus*]

8. Cells of leaf middle 41–55 µm wide × 48–70 µm long, with trigones minute to small; stem always smooth; ventral margin of leaf uniformly entire . . . [variable-leaved populations of *Lamellocolea*]

7. Underleaf disc margin entire or 1–3-dentate, only occasionally with 1 of processes ciliiform; gemmae occasional . . . . *C. novaezeelandiae* (p. 75)

6. Underleaf discs plane or convex (ventral view) 9

9. Leaf apices rather constant: rounded to truncate, only in weaker plants retuse to bidentate; gynoecia often on short, abbreviated, lateral-intercalary branches lacking normal leaves 10

10. ♀ Bracteole 0.2–0.4 bract area; perianth lobes entire or sparsely denticulate, at most with 2 lobes short bifid . . . . *C. fertilis* (p. 107)

10. ♀ Bracteole 0.6 or more bract area; perianth lobes all distinctly bifid 11

11. Leaves with margins uniformly entire, the apices retuse to bidentate on weak or depauperate plants, the apices otherwise devoid of other armature; branching of sterile shoots both terminal and intercalary, with terminal branches varying from 30–90% in frequency . . . 12

12. Underleaf disc lateral armature well developed: mostly laciniate to lobulate; trigones minute to small, only occasionally medium and straight sided; underleaves often 1.5–3× stem width; plants translucent; oil-bodies hyaline and glistening, 2–3(4) per cell, mostly elliptic to fusiform . . . . *C. semiteres* (p. 91)

12. Underleaf disc lateral armature reduced: mostly dentiform to ciliiform or lacking, only sporadically small-laciniiform; trigones normally large and bulging to knot-like (in shade forms medium and straight sided to weakly bulging); underleaves normally 1–1.5× stem width; plants dull-opaque; oil-bodies greyish orange, 3–7(9) per cell, nearly always spherical . . . . *C. canaliculatus* (p. 103)

11. Leaves, at least in some instances on any given shoot, armed with 1 or more coarse teeth; branching of sterile shoots all or nearly all lateral-intercalary (95–100%), terminal branches sporadic or lacking . . . . *C. rupicola* (p. 110)

9. Leaf apices polymorphic: rounded to truncate to retuse to 1- to 2-lobed; gynoecia on leading shoots with at least a few cycles of normal leaves 13

13. Plants small, 0.5–1 mm wide, often pale brown (at least in herbarium); terminal branching prevalent; leaves bordered by 1 (locally 2) rows of larger cells; underleaves 0.9–1.8× stem width; gynoecia always on main shoot; plants of calcareous substrates . . . . *C. calcareus* (p. 87)

13. Plants larger, to 2 mm wide, pale green; terminal branching lacking; leaves without a border; underleaves 1.6–2.8× stem width; gynoecia often on lateral-intercalary branches; plants of noncalcareous substrates . . . . *C. hattorii* (p. 84)

Chiloscyphus **subg.** ***Notholophocoleus*** (R. M. Schust.) J. J. Engel & R. M. Schust.

Lophocolea subg. *Notholophocolea* R. M. Schust., Hep. Anthoc. N. Amer. 4: 183. 1980.
Chiloscyphus subg. *Notholophocoleus* (R. M. Schust.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 410. 1985 (1984). Type: *Lophocolea boveana* C. Massal.

Plants suberect to erect, isophyllous to anisophyllous; branching of ventral- and lateral-intercalary types, also of *Frullania* type; leaves smooth, alternate, the apex undivided, entire or, less often, with a tooth; underleaves free or connate on 1 side, the apex undivided and entire to 1-dentate to retuse-bidentate to bifid to 0.3, the lamina margins entire or with a tooth. Plants dioecious. Antheridial stalk 1-, 2-, or 4-seriate.

The subgenus has three species, one amphipacific; the other two are restricted to southern South America (see Engel, 1992b, for a revision).

Sect. ***Notholophocoleus*** J. J. Engel, **sect. nov.**

Apex folii integer vel interdum dente praeditus; amphigastria in latere altero connata, apice simplici integroque vel retuso-bidentato vel bifido usque ad 0.3 partem longitudinis. Stipes antheridialis 1- vel 2-seriatus.

TYPE—*Lophocolea boveana* C. Massal.

Leaf apex entire or, sporadically, with a tooth. Underleaves connate on 1 side; apex undivided and entire to retuse-bidentate to bifid to 0.3. Antheridial stalk 1- (in ours) or 2-seriate.

Two species belong here, one (*C. boveanus* (C. Massal.) J. J. Engel & R. M. Schust.) in southern South America; the other (*C. austrigenus*) is amphipacific.

Chiloscyphus austrigenus (Hook. f. & Taylor) J. J. Engel & R. M. Schust.

Jungermannia austrigena Hook. f. & Taylor, London J. Bot. 3: 466. 1844. *Lophocolea austrigena* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 702. 1847. *Chiloscyphus austrigenus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 411. 1985 (1984). Type: Chile, Prov. Magallanes, Isla Hermite and/or Cabo de Hornos, *Hooker s.n.* (BM!–c. per.; NY!–c. per.; S!).

Plants stiff and wiry to rather flexuous and spongy, sometimes clasmatocoleoid in appearance, anisophyllous to subisophyllous, erect, bright light green to pure green (in herb. often fuscous except in distal sector), often forming a densely interwoven basal mass of wire-like leafless shoots that trap

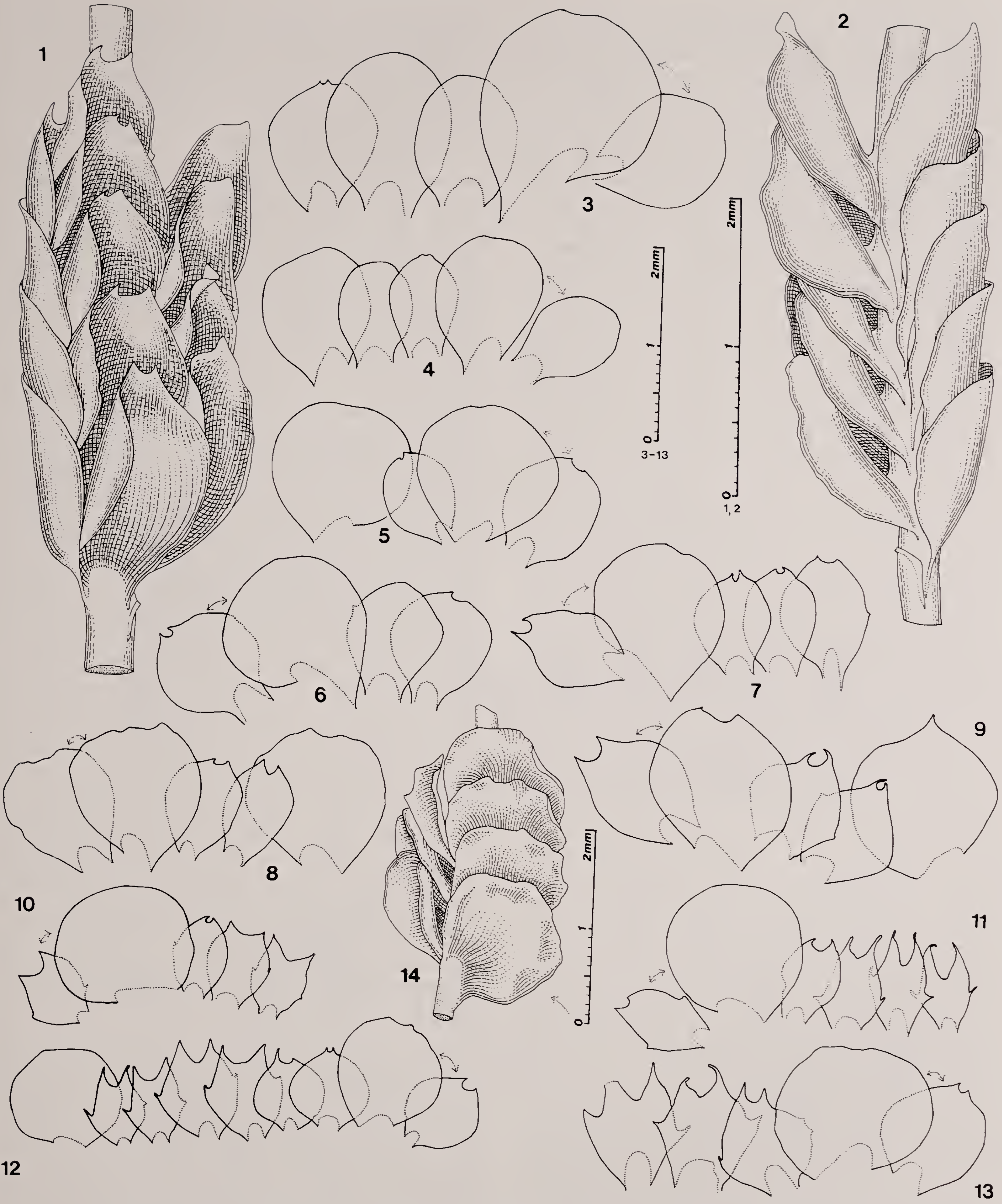


FIG. 2. *Chiloscyphus austrigenus* subsp. *okaritanus* (Steph.) J. J. Engel. **1.** Portion of shoot, ventral view. **2.** Portion of shoot, dorsal view. **3–13.** Leaves and underleaves, those indicated by an arrow are from same leaf–underleaf gyre; **3–7.** from optimal phase; **8–13.** from mod. *retusifolia-undulifolia* (details of underleaf connation not shown). **14.** Portion of shoot, lateral view. (**1, 2, 9,** from *Engel 14954*, Tasmania, Kelly Basin Road; **3,** from *Engel 13667*, Tasmania, Mt. Eliza; **4,** from *O. Schuster 65*, New Zealand, Fiordland Natl. Park; **5,** from *Engel 13999*, Tasmania, Ballroom Forest; **6,** from *Engel 16288*, Tasmania, Mt. Rufus Canal Road; **7,** from *Engel 14122*, Tasmania, Marigold Creek; **8, 14,** from *Engel 16297*, Tasmania, Mt. Rufus Canal Road; **10,** from *Engel 14395*, Tasmania, Rodway Range; **11,** from *Norris 27412*, Tasmania, Lake Lea; **12,** from *Norris 27060*, Tasmania, Adamson's Peak; **13,** from *Engel 14620*, Tasmania, Gordon River.)

fine gravel; shoots to 2 mm wide. Branches frequent, often copious, of ventral- or lateral-intercalary type and then just dorsal to axil of leaf–underleaf, the branches also of *Frullania* type, the half-leaf of same general shape as vegetative leaves; ventral-intercalary and *Frullania*-type branches of about equal frequency, lateral-intercalary branches a bit less common. Stem often narrow for plant size, 11–15 cells high, the cortex moderately well differentiated, in 1–2 layers of thick-walled cells; medullary cells with walls somewhat thickened. Rhizoids sporadic, from stem at immediate base of underleaf. Leaves alternate, orientation variable (often even on a single shoot): subhorizontal to vertical, often dorsally assurgent, erect to widely spreading; leaves contiguous to imbricate, free dorsally, orientation subtransverse to subsuccubous, the insertion succubous, distinctly J-shaped to merely weakly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves convex to plane to concave (but only rarely conchiform-concave), sometimes with leaves on 1 side of shoot concave and leaves on opposing side of shoot broadly convex, the leaves subsymmetrically to symmetrically orbicular to oblate; apex undivided but variable: broadly rounded to truncate to retuse, usually entire to repand to (occasionally) subsinuate, sporadically with a tooth, rarely isolated leaves retuse-short bilobed and never consistently so, the apex and margins sometimes undulate; dorsal margin broadly rounded, entire, short decurrent; ventral margin broadly rounded, sometimes more strongly so than the dorsal margin, sometimes dilated in basal sector and then subauriculate, the margin plane, entire. Leaf cells with a slight tendency toward tiering, the walls thin to slightly thickened, occasionally evenly so, trigones mostly small to medium, the sides straight to slightly bulging, the trigones occasionally large to bulging, but not strongly so; median leaf cells (11)16–24 μm wide, (12)19–30(37) μm long (subsp. *okaritanus*) or 22–34 μm wide, 28–40 μm long (subsp. *austrigenus*). Oil-bodies occupying fraction of cell lumen, hyaline, 2 or 2–3(4) per cell, globose to ovoid to rather wide elliptic, sporadically sublinear, coarsely granular, the globules to 2 μm in diam., the oil-bodies, mostly 7.2–9.8 × 4.6–5.9 μm, less frequently 11.1 × 5.2–5.9 μm, subglobose ones 5.9–6.5 μm in diam. Underleaves in well-developed plants somewhat smaller than leaves and much wider than stem (to 3.7× stem width), but in suboptimal plants much smaller than leaves and only slightly wider than stem; underleaves narrowly connate on 1 side, occasionally weakly so (especially in subisophyllous plants), the insertion basically inverted U-shaped, and because of connation, the opposing free margin of underleaf extends to varying degrees farther down stem than on connate side, the underleaf insertion thus appearing much like the leaf insertion and may be J-shaped; underleaves spreading, sometimes widely so, sometimes secund, imbricate, unistratose, optimally concave (particularly toward the base) to canaliculate, sometimes asymmetrically so and then with 1 side more reflexed than the other, the underleaves sometimes plane in weaker plants, exceptionally convex, the underleaves orbicular to elliptic to obovate, less often ovate, occasionally strikingly similar to leaf shape; apex with undivided and entire apices vary from rounded to truncate to retuse, but this condition grades to apices varying from retuse-bidentate to bifid to 0.3; lamina margins normally recurved, entire or with a small to large tooth, short to long decurrent on 1 side.

Asexual reproduction absent.

Plants dioecious. Androecia on leading shoots or elongate *Frullania*-type or ventral-intercalary branches that are initially terminal but eventually become intercalary; bracts similar to vegetative leaves in shape but variable in size: grading from somewhat to much smaller than leaves, the bracts erect, vertical, dorsally assurgent, loosely appressed to bract immediately above, free dorsally, ventricose in basal portion, the distal portion slightly concave, the apex and ventral margin entire; lobule somewhat variable in size, rather small to moderately large for bract size, the margin inflexed to involute, with a sharp dentiform to laciniiform projection, the margin otherwise crenulate and with several slime papillae; antheridia 1(2) per bract, the stalk short, uniseriate throughout or locally biseriate. Gynoecia on main shoot and long *Frullania* and ventral-intercalary branches, becoming increasingly more isophyllous toward the perianth and finally becoming nearly isophyllous; subfloral innovations of fertilized gynoecia not seen but sometimes with intercalary branches from axils of bracts and bracteoles of unfertilized gynoecia, the innovations often in turn producing gynoecia that again innovate; vestigial stem perigynium present, with 1(2) pairs of bracts and bracteoles inserted on it. Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free from one another, plane or distinctly concave, orbicular to elliptic; apex sinuate to retuse to retuse-(asymmetrically)bidentate, the apex otherwise entire; lamina margins plane or slightly reflexed distally, entire or denticulate; lamina with a median field of enlarged elongate cells in basal 0.3–0.5. Bracteoles of innermost series free (due to activity of stem perigynium) to connate on 1 side (sometimes strongly so), the bracteoles strongly concave distally but only slightly so toward base (ventral view), orbicular to broadly obovate to narrowly ovate; apex truncate and entire to truncate-bidentate (the teeth sometimes of only a few cells) to retuse-bidentate (often asymmetrically so); lamina margins entire or sparingly denticulate; lamina with field of enlarged elongate cells as in bracts. Perianth slightly to distinctly exserted beyond bracts, sharply trigonous throughout, the sides unistratose, the keels multistratose, the perianths narrowly elliptic, faintly narrowing toward the wide, distinctly 3-lobed mouth; lobes retuse to retuse-bidentate to very short bifid, the lobes otherwise entire or with several small teeth; keels sharp, with keelar wings common, of a few cells high and with a few teeth or ciliiform projections; perianth surface often with longitudinally oriented, low lamellae of varying lengths that are armed with teeth or cilia that often extend free distally as long, sinuous, ciliiform projections. Calyptra small, extending to ca. 0.6 the perianth length.

Seta 10–11 cells in diam., with 33 rows of outer cells surrounding an inner core of scattered, slightly smaller cells with corners thickened as in medium-sized trigones. Capsule elliptic to weakly obovate, 1085–1155 μm long, 735 μm wide, the wall 41–54 μm thick, of 5–6 (very locally 7) layers; outer layer of cells 24–30 μm, equal to 3.6 of interior strata or thicker than all of interior strata combined; outer layer of cells small, subquadrate, the radial walls thin, with magenta, small, nodular thickenings mostly on longitudinal walls and only sporadically on transverse walls, the exposed tangential wall distinctly thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layers thick walled, with vertical thickenings often considerably tangentially extended, the thickenings often restricted to lateral extremities

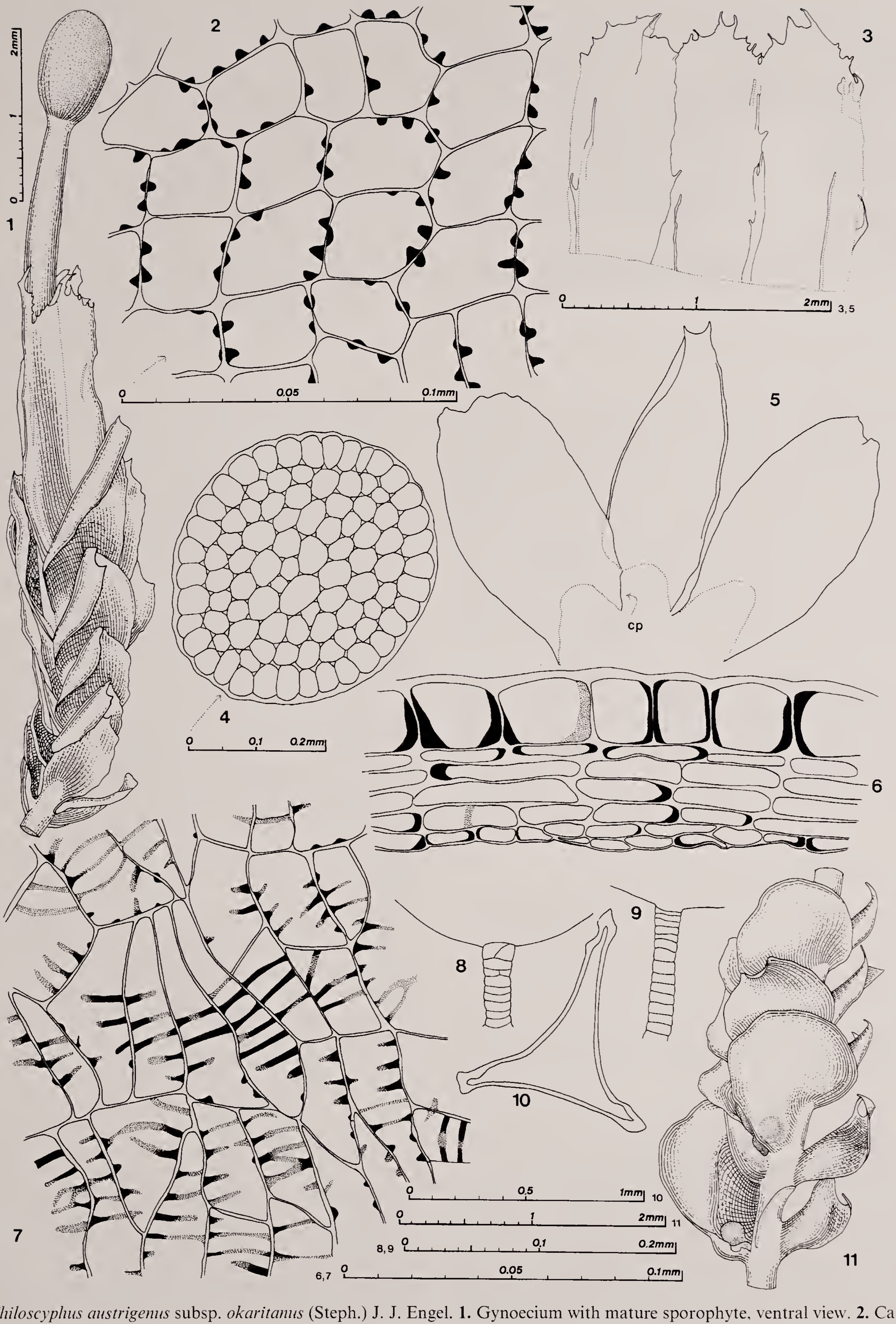


FIG. 3. *Chiloscyphus austrigenus* subsp. *okaritanus* (Steph.) J. J. Engel. **1.** Gynoecium with mature sporophyte, ventral view. **2.** Capsule wall, outer layer. **3.** Perianth (distal ca. two-thirds), ventral lobe in middle. **4.** Seta, cross section. **5.** ♀ Bracts and in middle, bracteole (cp = connate portion). **6.** Capsule wall, cross section. **7.** Capsule wall, inner layer. **8, 9.** Antheridial stalks. **10.** Perianth, cross section through median third. **11.** Androecium, dorsal-lateral view. (**1–7, 10,** from *Engel 17879*, New Zealand, below Mt. Shrimpton; **8, 11,** from *Engel 15639*, Tasmania, St. Valentines Peak; **9,** from *Engel 18977*, New Zealand, track to Alex Knob.)

TABLE 2. Comparison between *Chiloscyphus austrigenus* mod. *integrifolia-planifolia* and mod. *retusifolia-undulatifolia*.

Character	mod. *integrifolia-planifolia*	mod. *retusifolia-undulatifolia*
Leaf concavity/convexity	variable: slightly convex to plane to slightly concave	slightly concave, sometimes conchiform concave, less often convex
Underleaf concavity/convexity	distinctly concave to canaliculate (ventral view)	plane to slightly concave, less often sharply so
Underleaf apex	undivided and entire to retuse to retuse-bidentate, rarely short bifid (divided to ca. 0.15)	bifid to 0.1–0.3, sporadically retuse-bidentate
Underleaf lamina armature	usually entire, sporadically with a few-celled tooth	sometimes entire, typically with a small to well-developed tooth
Leaf undulation	none (plane)	undulate
Leaf apex	broadly rounded to truncate, occasionally faintly retuse, never with a tooth	truncate to sporadically rounded, ± narrowly repand to subsinuate, sometimes with a tooth, often retuse to retuse-1 dentate-lobate, occasionally retuse-short bilobed (the 2 lobes asymmetric)

of cells (cross section view) or absent altogether; innermost layer of cells highly irregular in orientation and shape, basically rectangular—some rather short and broad, others long and narrow, the walls thin, with semiannular bands yellow brown, common but very often incomplete, rather narrow and rather widely spaced from one another, the bands often faint and hardly discernable in median portion or throughout, sometimes forked but only occasionally anastomosing and then not delimiting fenestrae, the radial walls with nodular thickenings often present on both longitudinal and transverse walls, these often extending as short faint spurs.

Spores 11.5–12.4 μm yellow brown, thin, with faint, dense, low but sharply defined, close papillae and short-vermiculate markings; spore:elater diameter ratio 1.1–1.5:1. Elaters tortuous, 7.7–11 μm wide, tapered to tips, the spirals 2.4–2.9 μm wide, rather loosely wound.

The species is composed of two subspecies, as follows.

Key to the Subspecies of *Chiloscyphus austrigenus*

1. Median leaf cells (11)16–24 μm wide × (12)19–30(37) μm long; lobes of perianth mouth retuse-bidentate to very short bifid, never merely retuse, otherwise with several small teeth. New Zealand, Australia (Tasmania, Victoria, NSW) . . . . subsp. *okaritanus*
1. Median leaf cells 22–34 μm wide × 28–40 μm long; lobes of perianth mouth retuse to retuse-bidentate, otherwise entire. Southern South America . . . [subsp. *austrigenus*]

Chiloscyphus austrigenus (Hook. f. & Taylor) J. J. Engel & R. M. Schust., **subsp. *austrigenus***

For full synonymy of the typical subspecies, which is restricted to the American sector, see Engel (1990a, 1992b).

Chiloscyphus austrigenus* subsp. *okaritanus (Steph.) J. J. Engel

Lophocolea okaritana Steph., Bull. Herb. Boissier 6 (9): 785. 1906 (= Spec. Hep. 3: 85). *Chiloscyphus okaritanus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 420. 1985 (1984). *Chiloscyphus austrigenus* subsp. *okaritanus* (Steph.) J. J. Engel, J. Hattori Bot. Lab. 72: 113. 1992. Type: New Zealand, Okarito, *Kirk 592* (G!).

Lophocolea gunniana Nees *in* Gottsche, Lindenberg & Nees, Syn. Hep. 169. 1845, *syn. cf.* Hamlin (1973), *non Chiloscyphus gunnianus* Mitt. *in* Hooker f., Bot. Antarc. Voy. 3: 228. 1859. Type: Tasmania, Hampst[on] Hills, "in caespite *Agrostis intricata* et *Echinopog[onis] Gunniana*," Feb. 1838, *Gunn 1011* (STR!).

Lophocolea cordifolia Steph., Bull. Herb. Boissier 6(9): 789. 1906 (= Spec. Hep. 3: 89). *Chiloscyphus cordifolius* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 413. 1985 (1984), *nom. illeg. & syn. nov.*, *non C. cordifolius* Rodway, Pap. & Proc. Roy. Soc. Tasmania 1915: 106. 24 Feb. 1916 (see also vol. 2. of *Tasmania Bryophyta*, p. 54. 30 Aug. 1916) (= *Clasmatocolea notophylla* (Hook. f. & Taylor) Grolle). Type: Tasmania, West Coast, King River, *Moore 497* (G!, HO! ["sub no. 463"]).

Lophocolea austrigena fo. *bifida* Rodway, *Tasmanian Bryophyta*, vol. 2: 46. 30 August 1916 (preprint of Pap. & Proc. Roy. Soc. Tasmania 1916: 96. 19 Feb. 1917.), *syn. nov.* Lectotype (*nov.*) Tasmania, Cradle, Dec. 1915, *Rodway s.n.* (HO!).

DIFFERENTIATION—This subspecies is the sole member of subg. *Notholophocoleus* in Australasia. The subgenus otherwise occurs in southern South America (see Engel, 1992b).

The species shows some semblance to *C. novaezeelandiae*; for a discussion see under that species (p. 77).

VARIATION—This highly variable species has troublesome phases that provide both intrageneric and intergeneric (e.g., *Clasmatocolea*) problems. Table 2 contrasts the phases.

Both phases may at times be well-developed and robust. However, mod. *integrifolia-planifolia* is the optimal phase of the species. Such phenotypes are distinct and should offer no confusion with any other plant. This is not the case with mod. *retusifolia-undulatifolia*, and the boundaries of this phase must be understood to grasp the species. Particular care should be taken with plants having concave leaves because they are quite clasmatocoleoid in appearance. Indeed, plants with concave leaves and plane, narrow, more deeply divided underleaves bear a strong resemblance to *Clasmatocolea humilis* (Hook. f. & Taylor) Grolle. However, the following ensemble of characters of *Chiloscyphus austrigenus* will distinguish these plants from *C. humilis*: 1) underleaves sporadically or occasionally moderately concave (ventral view), 2) underleaves connate on 1 side, and 3) leaves sporadically at least weakly convex. Character 1 is sometimes particularly evident toward shoot apices. Because of the nature of the variability of the species, it is especially important that several or at times many different shoots be examined to determine relative expression of characters.

Phases with narrower, more deeply bifid underleaves often occur at sites where the plant is continuously saturated, such as on rocks at or below the water level of watercourses. Special care should be taken with plants from such habitats. In

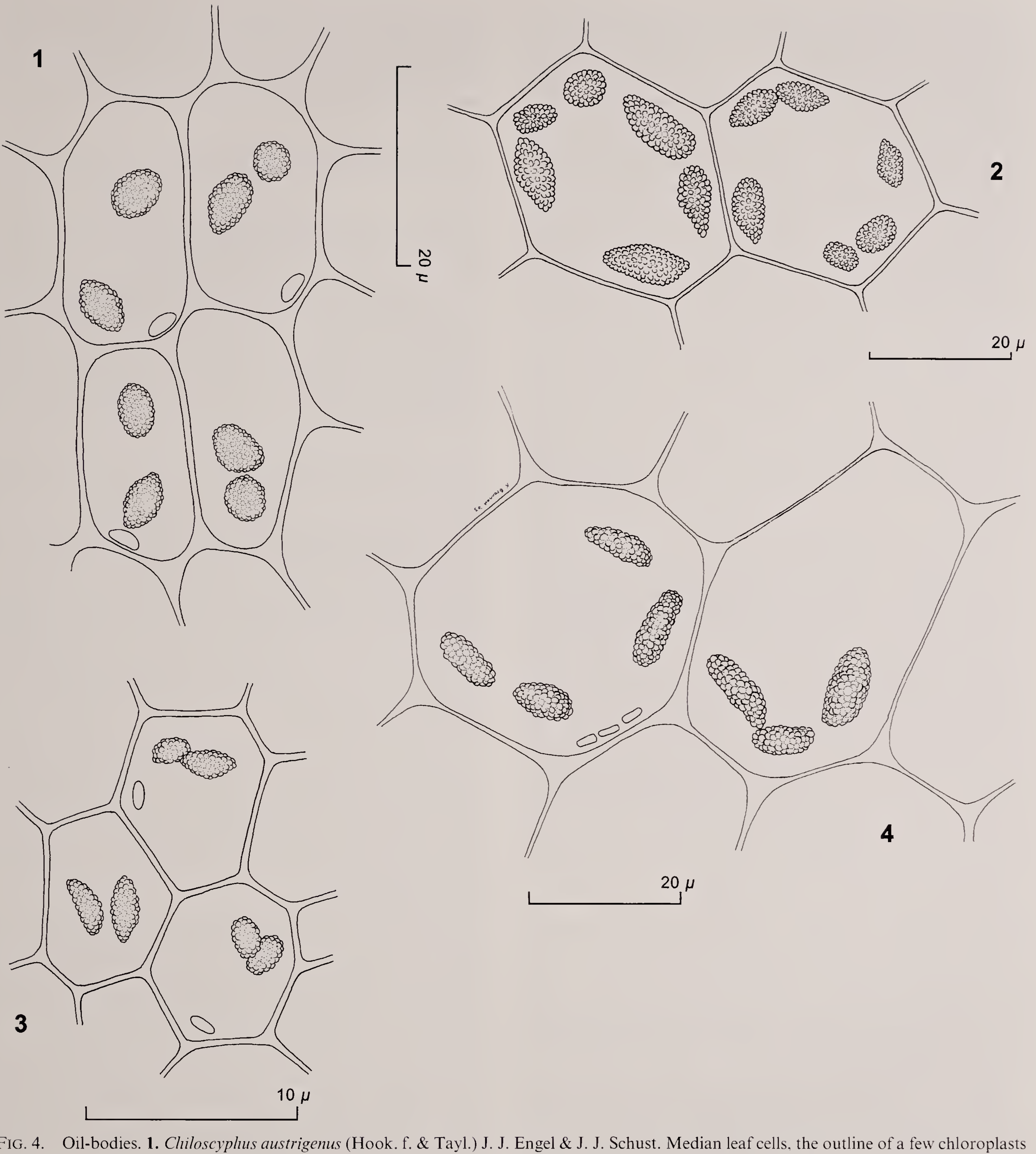


FIG. 4. Oil-bodies. **1.** *Chiloscyphus austrigenus* (Hook. f. & Tayl.) J. J. Engel & J. J. Schust. Median leaf cells, the outline of a few chloroplasts included. **2.** *Chiloscyphus lentus* (Hook. f. & Tayl.) Engel & Schust. Median lamina cells. **3.** *Chiloscyphus bispinosus* (Hook. f. & Tayl.) Engel & Schust. Median lamina cells, the outline of a few chloroplasts included. **4.** *Chiloscyphus bispinosus* (Hook. f. & Tayl.) Engel & Schust. Median lamina cells, the outline of a few chloroplasts included. (**1,** from *Engel, von Konrat & Braggins 24861*, New Zealand, South Is., Westland Prov., Lake Kaniere Scenic Reserve, Lake Kaniere Road; **2,** from *Engel 21174*, New Zealand, North Is., North Auckland Prov., Pohuehue Scenic Reserve; **3,** from *Engel & von Konrat 28097*, New Zealand, North Is., Southern North Is. Ecological Prov., NW Ruahine Range, vicinity between Makirikiri Tarns and Ruahine Corner Hut; **4,** from *Engel, von Konrat & Braggins 24991*, New Zealand, South Is., Nelson Prov., Mt. Arthur, Horseshoe Basin, near Tableland Track via Gordons Pyramid Peak.)

general, the deeper the underleaf sinus the greater the care required to differentiate the species. For example, phases of mod. *retusifolia-undulatifolia* should be treated with care to distinguish them from *C. novaezeelandiae* (for a discussion, see under that species). The key to undivided-leaved taxa also should be consulted (p. 11).

Phases of mod. *retusifolia-undulatifolia* occurring in shaded seepage areas at higher altitudes are especially troublesome.

Two collections from St. Valentines Peak, Tasmania, are relevant here. *Engel 15639*, which occurred on gravely soil in seepage areas in dwarf subalpine vegetation, is decidedly *Chiloscyphus austrigenus*-like in aspect. However, *Engel 15654*, from the same locality but on shaded gravely soil in seepage areas, has the distinct facies of *Clasmatocolea humilis*, complete with a high percentage of convex underleaves. *Engel 15777* is similar to the above *Clasmatocolea*-like plant; it occurred in a dripping mass on a shaded rock face under shrubby cover at 1250 m (Black Bluff, Tasmania). In such populations, a sparing number of shoots have gradation toward concave, shallowly divided underleaves more typical of *Chiloscyphus austrigenus*. In carefully working with such plants, one must also be aware that *Clasmatocolea humilis* is very rare in New Zealand and Tasmania, whereas *Chiloscyphus austrigenus* is common; plants thought to be *Clasmatocolea humilis* should therefore be treated with suspicion. This phase also occurs in New Zealand where it is found at variable altitudes. For example, it occurs in wet, rich *Nothofagus menziesii* forests, as in *Schuster 55681* from Lake Marion Track, Fiordland National Park, as well as alpine situations, where it forms pure carpets along the floor of rills, as in *Engel 17823* from Mt. Armstrong, Aspiring National Park.

Several interesting variants may occur within mod. *retusifolia-undulatifolia*. Shoots rather commonly have leaves on one side concave, erect, and vertical, whereas leaves on the opposing side of the shoot are broadly convex, obliquely to widely spreading, and subhorizontal (Fig. 2: 2). The leaves on the convex-leaved side have either the dorsal margin broadly reflexed or both dorsal and ventral margins broadly reflexed, the leaves then are canaliculate. This shoot asymmetry is often accompanied by asymmetry of underleaf concavity: the underleaves have one side more reflexed than the other side (Fig. 2: 1). Such shoots may have secund underleaves (*Schuster 67-3253*). The mod. *retusifolia-undulatifolia* phenotype also has another interesting characteristic: there often is a gradual torque of the axis, i.e., constant morphological dorsal and ventral sides of the plant are lacking. While unusual, this should not be surprising for an erect plant.

A rather rare variant of mod. *integrifolia-planifolia* may cause problems. This facies of the species has horizontal, strongly succubously oriented, wide leaves that have a weak cnemis. Such plants bear a striking resemblance to *Chiloscyphus semiteres* in dorsal view. These plants, which have underleaves typical of *C. austrigenus*, occur on rocks of stream and river bottoms, a typical *C. austrigenus* habitat. Examples of this phenotype are *Engel 14932* and *Norris 27895*; it is restricted to Tasmania.

NOTES—1) *Frullania*-type branching is far more prevalent in plants that are flexuous and spongy. On the other hand, intercalary branches are very common in stiff, wiry plants. Because the differences in texture are correlated with the amount of water associated with the niche, there seems to be a correlation of branch type with habitat.

2) Underleaf connation should be carefully checked in subisophyllous phases in that fusion is at times rather cryptic. I have found it helpful to remove a few underleaves and carefully rotate the axis to obtain a ventral-lateral view. Shoots lacking obvious leaf–underleaf connation have the underleaf base fused with the extreme base of the leaf (not necessarily at base of ventral margin) at the juncture with the stem and marked by a swelling of stem tissue.

3) All collections labeled *Lophocolea gunniana* collected by Rodway or determined by him are actually *C. semiteres*. This concept is reflected in the description of *L. gunniana* in Rodway (1916), especially in his statement that underleaves are 3/4 bifid (thus matching the condition in *C. semiteres*).

4) Hodgson (1953) confused this species with *Clasmatocolea* ("*Lophocolea*") *notophylla*; for a discussion see Engel (1980, p. 177).

NOTES ON TYPE SPECIMENS—1) *Lophocolea okaritana* Steph. The plants are rather stiff, with the leaves varying from convex to plane to concave, and the apex often 1-dentate to retuse-1-dentate; they represent mod. *retusifolia-undulatifolia*.

2) *Lophocolea gunniana* Nees. The plants represent mod. *integrifolia-planifolia*. The deeply concave underleaves are undivided and entire to retuse-bidentate to very short bifid at the summit. The plants are rather stiff, brownish, not readily rehydrating, and probably were not properly dried. Two probable types, both lacking nearly all relevant label data, are at S.

3) *Lophocolea cordifolia* Steph. The specimen is a mod. *integrifolia-planifolia*, and consists of flaccid, rather large plants.

4) *Lophocolea austrigena* fo. *bifida* Rodway. I have seen three Rodway-collected specimens labeled *L. austrigena* fo. *bifida* from Cradle Mtn., the only locality listed in the protologue. The collection of Dec. 1916 is mod. *integrifolia-planifolia* and consists of plants with retuse-bidentate underleaves. The other two specimens are mod. *retusifolia-undulatifolia*, one collected on Dec. 1915, the other Dec. 1916, and both agree with the protologue. Because the taxon was published on 30 August 1916, the Dec. 1915 specimen must be selected as lectotype.

DISTRIBUTION—The species has an amphi-pacific distribution (see Engel, 1992b). Subspecies *okaritanus* is Australasian and occurs on Auckland Island, New Zealand (Stewart Is.; South Is., sea level-1495 m; North Is., 1370–1495 m); Australia (Tasmania, sea level-1320 m; Victoria, 720–1265 m; New South Wales, 1780–2145 m). Within New Zealand the species appears to be very common on South Is. and rare and sporadic on North Is.

ECOLOGY—*Chiloscyphus austrigenus* subsp. *okaritanus* is common in forests of various types and is characteristic of watercourses, where it at times forms extensive, often pure carpets. It occurs on creek or stream bed rocks, where it may be submerged or above water level, as well as on rocks, boulders and, occasionally, soil (often gravely) of stream banks. The plants may occur on rocks associated with fast-moving water of cascades or waterfalls, or those merely wet from dripping, seepage areas or drainage channels. However, in all of these situations some accumulation of soil or silt is commonly present. Such watercourses may be without moving water at certain times of the year.

The subspecies is also rather common in the subalpine and alpine zones. Here it occurs in small watercourses such as streams and occupies niches similar to those associated with forests. It is rather common on rill bottoms (and then at times submerged) or at rill margins, sometimes deep under overhangs and similar protective niches. The subspecies also occurs over soil (sometimes quite gravely) of boggy or seepage areas (especially those on slopes) in drainage channels between boulders, and at the margins of pools and small lakes.

The subspecies only exceptionally occurs in niches not associated with watercourses. In forests, it may occur on moist, shaded boulders or rock outcrops or on earth. In alpine areas it may occur over soil in pockets between rocks within mosaics of boulder fields and vegetation.

On Auckland Is., the subspecies may occur on rocks at landing sites where it is washed by spray, thus tolerating salt spray (see Engel and Schuster, 1973).

Specimens Seen (selected)—**AUCKLAND IS.:** Disappointment Is., Castaways Bay, *Macmillan 83/144* (F); Ranui Cove, *Fineran 1951* (CHR); Tandys Inlet, *Wenham s.n.* as *L. planiuscula* (CHR); Tuckers Point, *Fineran 1729* (CHR); northern coast, Ewing Is., *Fineran 1998* as *L. planiuscula* (CHR). **NEW ZEALAND. STEWART IS.:** Port Pegasus, vicinity of Tin Range Track, ca. 100–200 m, *Engel, von Konrat and Braggins 24202* (F); Pegasus Harbour, along Pegasus Creek, 0.5–1 mi. above mouth, 30–60 m, *Schuster 59813* (F); Tin Range, *Schuster et al. s.n.* (CHR); Glory Harbour, *Martin 311* (CHR). **SOUTH ISLAND. SOUTHLAND:** Fiordland, SE of Lake Shirley, 915 m, *Given 69456, 69458*–c. ♂, both as *L. planiuscula* (CHR); Fiordland Natl. Park, head of Lake Manapouri, *Simpson s.n.* (CHR); ibid., head of Lake Manapouri to Wilmot Pass, *Simpson s.n.* (CHR); ibid., Warm Lake Manapouri, ca. 185 m, *Johnson 240* (CHR); ibid., Wilmot Pass Road to Deep Cove, ca. 305 m, *Child H 5601* as *L. gunniana* (F); ibid., Stuart Mtns., W shore of Lake Thomson N of stream draining from Lake Wade, *Fife 7627b* (F); ibid., Falls Creek, *Morice et al. s.n.*–c. ♂ + per. (CHR); ibid., Milford Track, E of Mackinnon Pass, *O. Schuster 53*–c. ♂, *55* (F); ibid., Lake Marian Track, on Hollyford River, at foot of Christina, *Schuster 55681* (F); ibid., Milford Track, ca. 3 mi. beyond Quintin Huts, *Morice et al. s.n.*–c. ♂ (CHR); ibid., Milford Sound Track, between Quintin Hut in Arthur Valley and Boat Landing on Milford Sound, *O. Schuster 65, 75* (F); ibid., Milford Sound, track to Bowen Falls, sea level, *Engel 22008*–c. ♂ (F); same loc., *Morice et al. s.n.*–c. ♂ (CHR); ibid., 2 km from Milford Sound, *Horner s.n.* (AK); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18856*–c. per. (F). **OTAGO:** Catlins River area, Ajax Swamp, ca. 1 km N of Ajax Hill, ca. 455 m, *Child H 5521* as *L. gunniana*–c. per. (F); Maungatua, *Simpson s.n.* (CHR); near Berwick, S of Dunedin, *Allison H854* as *L. planiuscula* (CHR); Cargill, Dunedin, 455 m, *Child 1535* as *L. gunniana*–c. per. (CHR); Lee Stream, Otago, 300 m, *Child 2509* as *L. planiuscula* (CHR); Fiordland Natl. Park, trail between Gunn's Hut and Hidden Falls, ca. 30 mi, SE of Lake McKerrow, *Hatcher 608, 627, 639* (F); Aspiring Natl. Park, below and W of Shrimpton, ca. 1220–1370 m, *Child H 4154, H 4155, H 4161* all as *L. gunniana* (F); ibid., ibid., 1370–1470 m, *Engel 17879*–c. sporo. (F). **WESTLAND:** Aspiring Natl. Park, below and W of Armstrong, SSW of Brewster, 1250–1450 m, *Engel 17823*–c. per. (F); ibid., Cross Creek, 1 km N of Haast Pass, 510 m, *Engel 23121*–c. ♂ + per. (F); Haast Pass to Haast Road, about 4 km NW of Haast Pass, *Mues NZ 130* (F); Jackson Bay, between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, ca. 30 m, *Child H 4230* as *L. gunniana* (F); 20 km S of Fox Glacier, ca. 30 m, *Child H 3725* (F); Fox Glacier, on trail to Cone Rock, *Schuster 67-3253* (F); Westland Natl. Park, track to Lake Gault, NE of Lake Matheson, NW of town of Fox Glacier, ca. 100–200 m, *Engel 21700* (F); ibid., track to Alex Knob, off track to Louisa Peak, 1170 m, *Engel 18977*–c. per. + ♂ (F); Franz Josef Glacier, *Allison s.n.* (CHR); Okarito, *A. H. s.n.* as *L. novaezeelandiae, 592* (CHR); Kelly's Hill, Otira, *Martin s.n.* as *L. novaezeelandiae* (CHR); Lake Brunner, *Visch 113pp*–c. ♂ + per. (CHR); Paparoa Mtns., N flank of Euclid, 1100 m, *Beever s.n.* (AK); ibid., ibid., ca. 0.5 km SE of Morgan Tarn, 1005–1065 m, *Fife 6421* (F). **CANTERBURY:** Arthur's Pass Natl. Park, just above village of Arthur's Pass, near start of Punchbowl Creek Track, *Engel 6915* (F). **NELSON:** Maimai State Forest, 3 mi. NW of Reefton, 280–350 m, *Macmillan 76/100* as *L. semiteres* (CHR); Nelson Lakes Natl. Park, NW flank of St. Arnaud Range, on "Loop Track," near eastern shore of Kerr Bay, Lake Rotoiti, *Fife 6791a* (F); Matakitaki River Valley, 6–7 mi. S of Murchison, *Schuster 50690*–c. ♂ (F); near Gibbs, ca. 1495 m, *Brown 88/129f* as *Clasmatocolea humilis* (AK); Flora–Salisbury Track, ca. 1040 m, *Brown 88/62* (AK); Hope Range, *Brown 88/2b* as *L. novaezeelandiae* (AK); Pupu Spring, Takaka, *Michaelis s.n.* (CHR). **MARLBOROUGH:** Fishtail, ca. 1220 m, *Child H 4342* as *L. gunniana* (F); Pelorus Bridge, *Braggins s.n.* (AK). **NORTH ISLAND. WELLINGTON:** W Ruahine Mtns., Whanahuia Range, 1–1.5 mi. W of Mangahuia, ca. 1370 m, *Schuster 67-572A, 67-577* (F); ibid., ibid., 0.5 mi. N of Mangahuia, 1465–1495 m, *Schuster 67-633* (F). **GISBORNE:** Raukumara Range, Raukumara Forest Park, vicinity of peak of Raukumara, ca. 1350 m, *Engel and von Konrat 27942* (F). **SOUTH AUCKLAND:** Base of Coromandel Peninsula, *Mitchell s.n.*–c. per. + ♂ (CHR). **TASMANIA.** Port Arthur, *Rodway s.n.* as *L. macrostipula* (HO); Adamsons Peak, 1065 m, *Rodway s.n.*–c. ♂ (HO); along trail to Adamsons Peak, from the hut to the peak, ca. 800–1200 m, *Norris 27060* (F); ibid., between Manuka Flat and the hut, 500–800 m, *Norris 27051*–c. sporo. (F); Geeveston, *Rodway s.n.* as *L. cordifolia* (HO); Hartz Track, *Rodway s.n.*–c. per. (HO); Hartz Mtn. Natl. Park, Lake Esperance, SE of base of Hartz Mtns., head of Esperance River, ca. 975 m, *Schuster 50174* (F); Wellington, near Pipeline Track, *Ratkowsky 79/95* as *L. gunniana*–c. sporo. (HO); ibid., St. Crispins, 610 m, *Weymouth 506*–c. ♂, *510, 570, 578* (all as *L. gunniana*) (HO); ibid., Millhouse's Creek, St. Crispin's Track, *Weymouth 512* as *L. gunniana* (HO); ibid., Snake Plains, *Ratkowsky 80/66, s.n.* (HO); ibid., Deep Creek, 490 m, *Weymouth 287* as *L. gunniana*–c. ♂ (HO); ibid., plateau, 1220 m, *Rodway s.n.*–c. ♂ (HO); ibid., ibid., 1280 m, *Engel 16363*–c. ♂ (F); ibid., ibid., *Ratkowsky H 1375* as *L. gunniana, 79/98*, as *L. gunniana*–c. ♂ + per. (HO); ibid., ibid., *Rodway s.n.* as *L. cordifolia* (HO); ibid., Dead Island Bogs, ca. 1200 m, *Ratkowsky H 1378* as *L. gunniana* (HO); Margate, *Rodway s.n.* as *L. cordifolia* (HO); Field Natl. Park, Rodway Range, between Rodway Ski Tow and K Col area, 1240–1310 m, *Engel 14395* (F); plateau region E and SE of Eliza summit, E of Lake Pedder, ca. 1225 m, *Engel 13667*–c. per. (F); Tim Shea, *Ratkowsky H 1381* as *L. gunniana* (HO); Sentinels Track to Lake Pedder, 400 m, *Ratkowsky 78/76* as *L. gunniana* (HO); Gordon River, vicinity of Sir John Falls, just up river from Butler Is., ca. 50 m, *Engel 14758*–c. ♂ (F); ibid., Pine Landing, 6 mi. from river mouth and Macquarie Harbour, sea level, *Engel 14620*–c. per. (F); terminus of Rufus Canal Road, S of Rufus and Lake St. Clair, 750 m, *Engel 16297*–c. per. + ♂ (F); Cradle–Lake St. Clair Natl. Park, Rufus, *Ratkowsky 79/13* as *L. gunniana* (HO); ibid., on W shores of Lake St. Clair about 3 mi. N of ranger station on trail to Echo Point, ca. 750 m, *Norris 27895* (F); Griffiths Creek (tributary of Surprise River), ESE of Arrowsmith, 1.7 km via Lyell Highway W of King William Saddle and 17.4 km W of Derwent Bridge, 700–720 m, *Engel 19485* (F); Kelly Basin Road, between junction with Franklin River Road and Kelly Basin, above Nora River, 90 m, *Engel 14954* (F); King River, 11.3 km by road from Regatta Point and 13.3 km by road from Strahan Harbour, sea level, *Engel 14932*–c. per. + ♂ (F); Dubbilbarril, King River, *Weymouth 1082* as *L. cordifolia* (HO); Purgatory Gap, S of Queenstown, *Norris 33615* (F); Cool Creek at Lyell Highway, *Norris 33419* (F); Cradle–Lake St. Clair Natl. Park, Cradle, *Rodway s.n.*–c. ♂, *s.n.*–c. sporo (HO); ibid., central plateau, *Ratkowsky H 1382* as *L. gunniana* (HO); ibid., Ballroom Forest, SW side of Lake Dove, 950–1050 m, *Engel 14018*–c. ♂ (F); ibid., Marigold Creek, W of and draining into Crater Lake, vicinity of Crater Peak Lookout, 1250 m, *Engel 14122*–c. ♂ (F); ibid., Plateau Creek, between Overland Track and Kitchen Hut Track, W of N end of Lake Dove, 1250 m, *Engel 19658* (F); ibid., Weindorfers Forest, ca. 920–1080 m, *Jarman 88/17, 88/18, 88/19* all as *C. okaritanus* (F); ibid., ibid., along track from Waldheim Chalet to Hounslow Heath Track, 975 m, *Engel 14043*–c. sporo. (F); forest on S shores Lake Lea, ca. 800 m, *Norris 27412, 27486* (F); Black Bluff, just below summit, S of Burnie, 1250–1320 m, *Engel 15777* (F); SW slope of St. Valentines Peak, SSW of Burnie, 920–1100 m, *Engel 15639*–c. ♂ (F); Hellyer Gorge picnic area, *Norris 33892B* (F); Sassafras Creek, about 3 mi. W of Mole Creek, ca. 300 m, *Norris 32840* (F); Dip Falls, Dip River off Mawbanna Road, S of Port Latta, 95 m, *Engel 19738* (F); Newhaven Road, just S of Doughboy Hill, 0.4 km E of junction with Mawbanna Road, S of Port Latta, 45 m, *Engel 19734* (F). **AUSTRALIA. VICTORIA:** Summit plateau of Baw Baw, N of Moe, E of Melbourne, 1265 m, *Engel 16893*–c. per. (F); Great Dividing Range, Watts River near Fernshaw, NE of Melbourne, *Engel 16762* (F); Bonang River, 59 km NE of Orbost, 720 m, *Streimann 10043*–c. ♂ (F). **NEW SOUTH WALES:** Kosciusko Natl. Park, Carruthers Peak, ca. 1830–2145 m, *McVean 26449, 26450*, both as *C. okaritanus* (F); ibid., ridge WSW of Charlotte Pass off road to Kosciusko, not far from Snowy River, 1780–1900 m, *Engel 17105, 17106* (F).

Chiloscyphus **subg.** ***Lophocolea*** (Dumort.) J. J. Engel & R. M. Schust.

Jungermannia sect. *Lophocolea* Dumort., Syll. Jungerm. Eur. 59. 1831. *Lophocolea* (Dumort.) Dumort., Recueil Observ. Jungerm. 17. 1835. *Chiloscyphus* subg. *Lophocolea* (Dumort.) J. J. Engel & R. M. Schust. *in* Engel, Phytologia 83: 42. 1998 (1997). Type: *Jungermannia bidentata* L.

Plants anisophyllous to subisophyllous. Branching mostly terminal-lateral and lateral-intercalary, with ventral-intercalary type rare or lacking (exc. *C. erosus*). Leaves smooth, alternate, the insertion lines usually extending to stem midline dorsally (a few species excepted); apex bifid, occasionally undivided, sometimes polymorphic (and then rounded to 1- to 2-lobed); margins entire or variously armed with teeth, cilia, or laciniae. Underleaves free or narrowly connate on 1 or both sides; apex bifid at least to 0.4 (exc. *C. aperticaulis* and sometimes in *C. mediinfrons* and *C. erosus*), often divided nearly to the base, the lamina margins with a process grading from dentiform to lobuliform, occasionally merely with 2–3 teeth. Asexual reproduction lacking or by 1–2(–4)-celled gemmae or caducous lobe tips. Plants dioecious or autoecious. Antheridial stalk 1-seriate. Capsule wall innermost cells with tangential thickenings that, if occasionally forked, do not delimit fenestrae.

The large subgenus occurs primarily in tropical and south temperate–subantarctic areas. Relatively few taxa are holarctic.

Chiloscyphus **sect.** ***Lophocolea*** (Dumort.) J. Hentschel

Chiloscyphus sect. *Lophocolea* (Dumort.) J. Hentschel, Pl. Syst. Evol. 262: 129. 2006.

Branching mostly terminal-lateral and lateral-intercalary, ventral-intercalary type rare or lacking (exc. *C. erosus*). Leaves fundamentally bifid; margins entire or variously armed with teeth, cilia, or laciniae. Underleaf apex bifid at least to 0.6 (exc. some populations of *C. erosus*), often divided nearly to the base; lamina margins with a process grading from dentiform to lobuliform. Asexual reproduction exceptional, by gemmae or caducous lobe tips or regenerant buds. Plants dioecious or autoecious. Gynoecia often on branches lacking vegetative leaves, often on terminal branches.

This section, world-wide in distribution, is restricted to plants with fundamentally bilobed leaves. In this respect the circumscription of sect. *Lophocolea* is essentially similar to that in Schuster (1980). I differ from Schuster (1980) in the inclusion of gemmiparous plants; Schuster accepts only gemmae-free plants for the section. Also likely belonging here is the gemmiparous species:

Chiloscyphus himalayensis (A. Srivast. & S. C. Srivast.) J. J. Engel, **comb. nov.**

Lophocolea himalayensis A. Srivast. & S. C. Srivast., Indian Geocalycaceae (Hepaticae) p. 182, pl. 56. 2002. Holotype: India, Western Himalayas, on way to Valley of Flowers, ca. 4000 m, *Srivastava et al. 4166l80* (LWU, *non vidi*).

A species from New Guinea probably also belongs here:

Chiloscyphus wambanus (Piippo) J. J. Engel, **comb. nov.**

Lophocolea wambana Piippo, Acta Bot. Fennica 131: 163, *f. 18d–j.* 1985. Holotype: Papua New Guinea, Morobe Prov., 1 km W of Lake Wamba, 2600 m, *Norris 64605* (H, *non vidi*). (See Piippo, 1985.)

Australasian taxa of sect. *Lophocolea* may be distinguished by the following key. However, particular care should be taken with plants of *Lamellocolea granditexta* (Steph.) J. J. Engel (Engel, 1991c), a relatively common New Zealand species that, when sterile, will key to this section. Sterile plants of this species may be distinguished from all Australasian Lophocoleaceae by the 1) large shoot size (shoots to 5.4 mm wide); 2) fundamentally bifid leaves that often show some tendency toward apex variability (Fig. 5: 6) and tend toward asymmetric dorsal connation (Fig. 5: 9); 3) nonprotracted leaf lobes, the uniseriate portion consisting of a row of, at most, 4(5) cells (Fig. 5: 7); 4) deeply bifid underleaves that are distinctly connate on 1 side, with the other side long decurrent and often connate (Fig. 5: 1); and 5) large leptodermous cells with minute to small trigones (Fig. 5: 2). Cells are 38–53 µm wide × 43–70 µm long in the leaf middle, and such magnitude is among the largest in the family. Careful search should be made for gynoecia in *Lamellocolea*, which have useful diagnostic characters that may be observed even when gynoecia are young. Search should be made for presence of perianth lamellae (Fig. 6: 1, 3, 8) together with the small innermost bracteole (Fig. 6: 6).

Key to the Australasian Species of Sect. ***Lophocolea***

1. Underleaves bifid to 0.4–0.6, the lamina margins commonly 1–3(4)-dentate; underleaves consistently concave (ventral view). Leaf lobe tips never piliform, the uniseriate row of less than 4 cells ..... [*C. novaezeelandiae* var. *grandistipulus*; cf. p. 83]
1. Underleaves bifid to at least 0.6, the lamina margins all or mostly each with a prominent laciniiform or lobe-like process; underleaves plane to convex (ventral view), isolated exceptions aside (or if concave, then the leaf lobe tips piliform, the uniseriate row of 4 or more cells) 2
    2. Leaf lobes with uniseriate row of cells caducous, the mature leaves with lobes terminating in 2(3) laterally juxtaposed cells that frequently possess secondary septa; gemmae present, at tips of leaf lobes and from regenerants; plants smaller, to 2.2 mm wide; leaf cell trigones often large and convex sided. Underleaves free (sometimes connate on 1 side in *C. erosus*) 3
        3. Leaf apex with form ± consistent throughout shoot (exc. at shoot tips, where lobes are complete): lobes with uniseriate row of cells caducous, the mature leaves with lobes terminating in 2(3) laterally juxtaposed cells that frequently possess secondary septa; leaves without accessory lobes at apex, never 4-lobed, never with complete loss of lobes; vegetative branches mostly of *Frullania* type, occasionally lateral intercalary, never ventral intercalary; shoots distally plane, neither cernuous nor flagelliform; stems narrow for plant size; ♀ never on ventral-intercalary branches. Tasmania (rather common); very rare in New Zealand (Auckland Is.; Campbell Is.; South Is.) .... *C. perpusillus* (p. 67)
        3. Leaf apex (gemmiparous leaves) becoming irregular and progressively more erose and, with continued gemmae formation, the lobes disappearing altogether (the leaf apex then ± broadly rounded); leaves often with 1–2 accessory lobes at apex lending a ragged appearance; vegetative branches all or mostly intercalary (both lateral

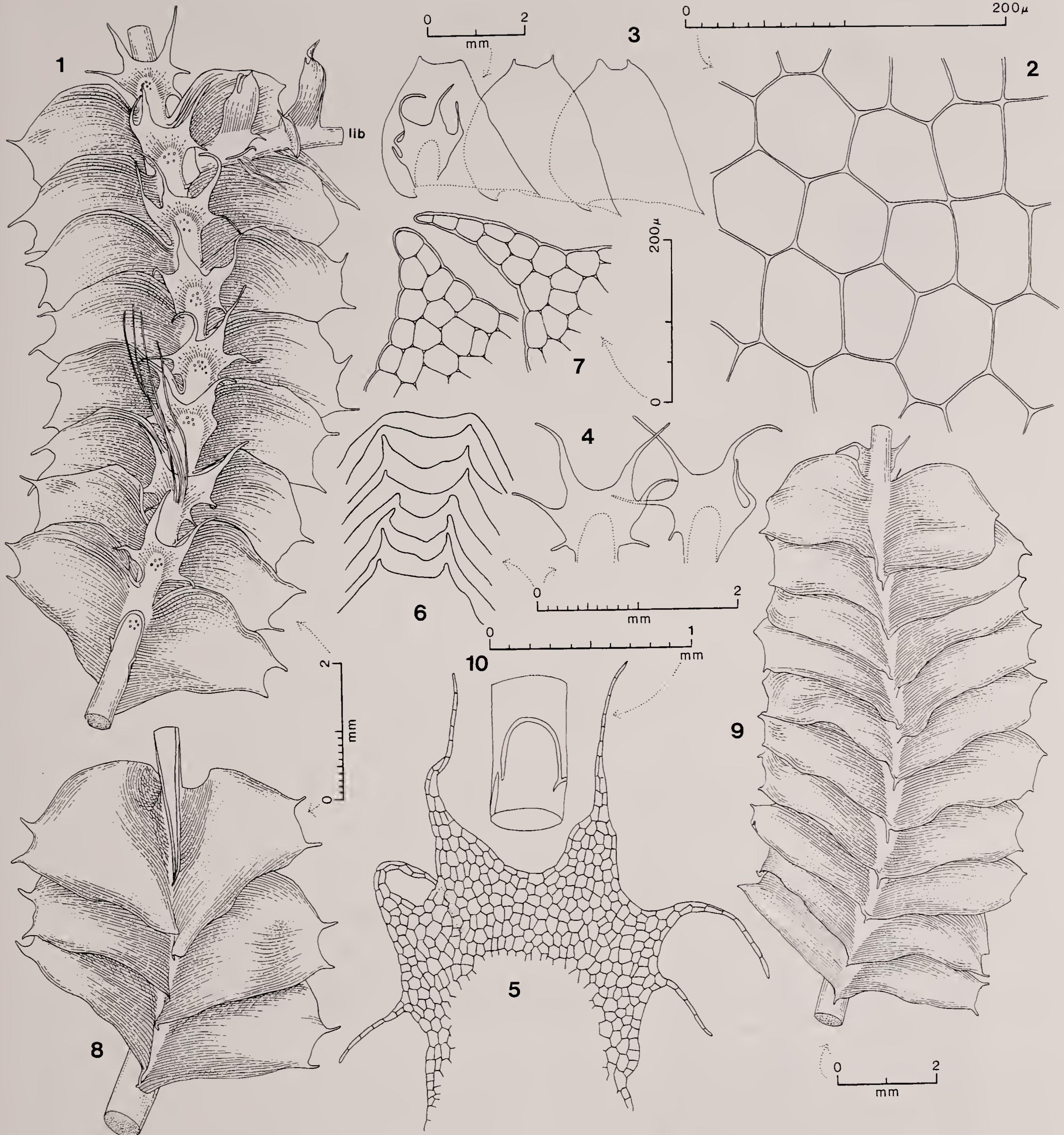


FIG. 5. *Lamellocolea granditexta* (Steph.) J. J. Engel. **1.** Portion of main shoot with lateral-intercalary branch (= LIB), ventral view; rhizoids cut for clarity at all but 2 leaf bases, but rhizoid origin indicated. **2.** Median leaf cells. **3.** Leaves and underleaf from same shoot and at same scale. **4.** Underleaves from 1 shoot. **5.** Underleaf. **6.** Apices from 8 consecutive leaves from 1 side of single shoot, at top from distalmost leaf. **7.** Distal sectors of ventral leaf lobes. **8.** Sector of shoot from population having nearly exclusively short-bilobed leaves, dorsal view. **9.** Portion of main shoot, dorsal view; note variation of leaf apex and leaf connation. **10.** Shoot segment showing details of insertion, ventral view. (**1–7, 9, 10,** from *Schuster 67-4131A*, New Zealand, South Is., Otago Prov., Table Hill Reservation; **8,** from *Child 1596*, New Zealand, South Is., Southland Prov., Lake Hauroko.)

and ventral); shoots distally often cernuous, sometimes becoming flagelliform; stems thick and fleshy for plant size; ♀ often on ventral-intercalary branches. Plants to 0.8 mm wide. New Zealand . . . . *C. erosus* (p. 72)

2. Leaf lobes persistent, terminating in a uniseriate row of (2–)5–11 cells lacking secondary septa; gemmae lacking; plants larger, to 4 mm wide; leaf cell trigones mostly minute to small to medium, only sporadically large and bulging 4

4. Underleaves free at least on side nearest to adjacent leaf base (occasionally weakly connate on 1 side in *C. anisolobus*) 5

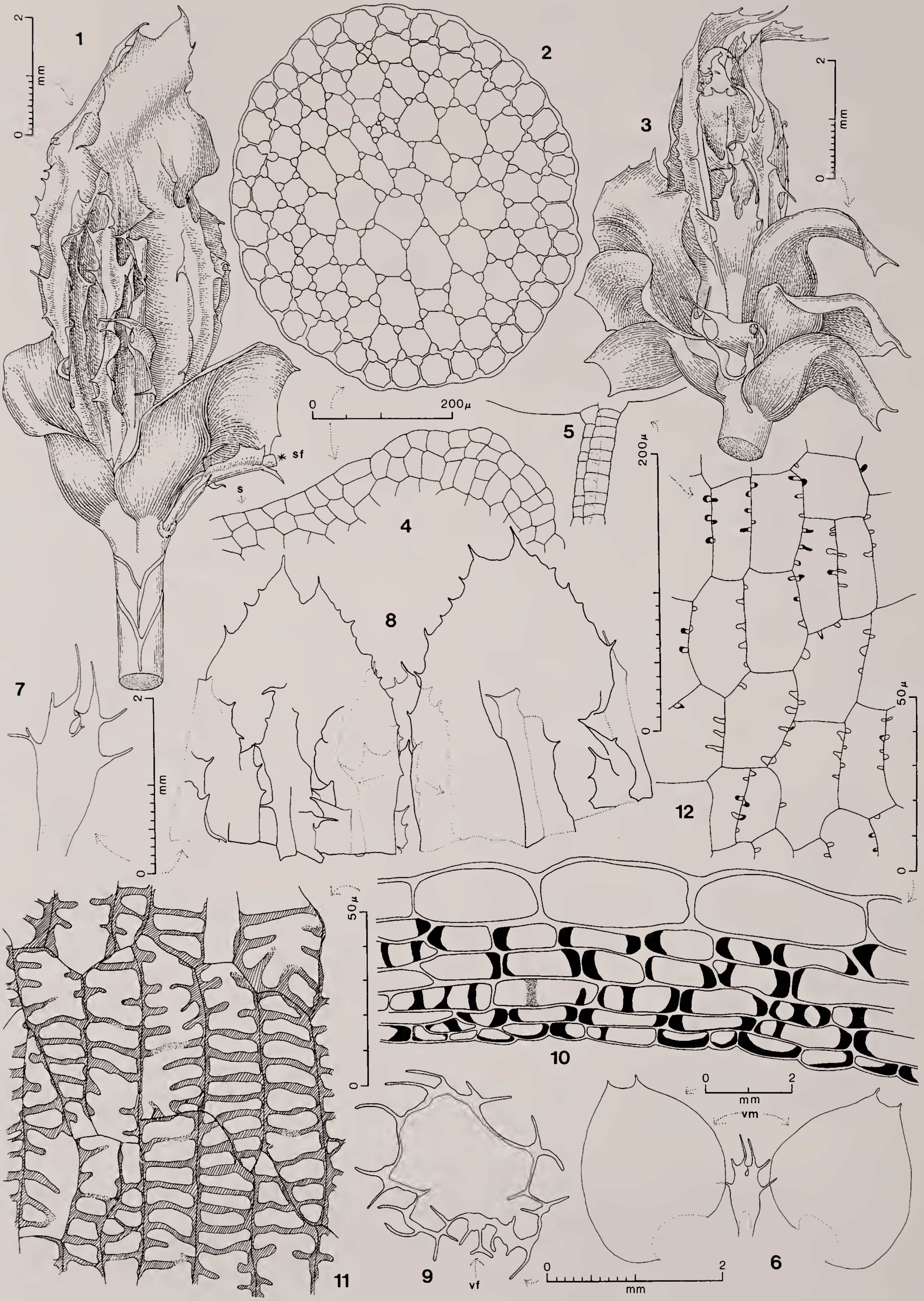


FIG. 6. *Lamellocolea granditexta* (Steph.) J. J. Engel. **1.** Gynoecium, dorsal view the bracts and bracteoles below those of innermost series removed for clarity (SF = subfloral innovation). **2.** Seta, cross section. **3.** Gynoecium and enclosed sporophyte, ventral view. **4.** Margin of ♂ bract lobule (S = sinus between lobe and lobule). **5.** Antheridial stalk. **6.** Bracts and bracteole to 1 scale (vm = ventral margin). **7.** Bracteole in Fig. 6 at higher magnification. **8.** Distal portion of perianth, ventral lobe mostly hidden by huge wings, the arrows indicate distalmost extent of "sutures" fusing the ventral to the lateral lobes, the ventral lobe free distal to arrows. **9.** Perianth, cross section (vf = ventral face); note lamellae on interior surface. **10.** Capsule wall, cross section. **11.** Capsule wall, inner layer. **12.** Capsule wall, outer layer. (**1,** from *Schuster 67-4131A*, New Zealand, South Is., Otago Prov., Table Hill Reservation; **2–12,** from *Child 1596*, New Zealand, South Is., Southland Prov., Lake Hauroko.)

5. Leaf insertion not attaining stem midline dorsally, a leaf-free gutter of (1)2–5 stem cells present; underleaves 0.95–1.5× stem width. Trigones lacking 6

6. Leaves often with accessory armature, the ventral margin often with a dentiform-lobuliform process in distal sector, the leaves then often trifid; leaf lobes terminating in a single cell or a uniseriate row of 2–3(4) cells; underleaf lobes terminating in a single cell or a uniseriate row of 2–3 (rarely 4) cells. Perianth cyathiform. New Zealand . . . . *C. anisolobus* (p. 63)

6. Leaves lacking accessory armature, never trifid; leaf lobes terminating in a single cell or a uniseriate row of 4–5 cells; underleaf lobes also longer, terminating in a uniseriate row of 4–9 cells. Australia (NSW) . . . . *C. excisifolius* (p. 61)

5. Leaf insertion attaining stem midline dorsally, no leaf-free gutter; underleaves 1.3–3.4× stem width 7

7. Dioecious, ♂ and perianths infrequent; leaves normally with a border of 1–2 rows of larger cells at least feebly developed. Leaf intramarginal cells often dimorphic: most small, but scattered among them are conspicuously enlarged cells 8

8. Leaves bifid to 0.4–0.55, the lobes often ventrally sulcate; underleaf lamina 2–4 cells high (between sinus base and underleaf base), the margins reflexed; leaf margins (both ventral and dorsal) often with 1–2(3) cilia or laciniae; trigones normally distinct, ranging from small/medium to medium/large; weak plants with leaf apices remaining uniformly bifid. New Zealand . . . . *C. bispinosus* (p. 31)

8. Leaves bifid to 0.15–0.3, the lobes uniformly plane, not ventrally sulcate; underleaf lamina (at least on well-developed shoots) 5–11 cells high (2–3 cells high in weaker plants), the margins usually plane, reflexed only in robust extremes (rare); leaf margins nearly always entire, very rarely with an isolated leaf 1-ciliate; trigones minute to small or lacking; weak plants with leaf apices polymorphic, sometimes 1-lobed to retuse. New Zealand, Tasmania, Australia . . . . *C. subporosus* (p. 40)

7. Autoecious, ♂ and perianths common; leaves lacking a border of larger cells. Leaf cells not dimorphic, without scattered enlarged intramarginal cells 9

9. Leaf margins normally entire, the ventral sporadically with 1(2) ciliiform projections, the dorsal margin and also the margin defining the sinus never armed; underleaves bifid, normally divided nearly to base, the lamina of only a few cells high and only rarely 5–7 cells high; underleaf median lobes 5–11 cells wide at base; oil-bodies coarsely papillose to finely botryoidal. New Zealand; in Tasmania not above 650 m . . . . *C. cuspidatus* (p. 50)

9. Leaf margins often armed: the ventral frequently with 1–2(3) ciliiform-laciniiform processes, the dorsal margin and also the margin defining the sinus sometimes with a cilium; underleaves weakly to distinctly 4-lobed (optimal plants, bifid in suboptimal plants), the lamina often distinct and then 6–15 cells high; underleaf median lobes 9–17(24) cells wide at base; oil-bodies coarsely botryoidal, the spherules distinct, large. Tasmania, above 900 m . . . . *C. longiciliatus* (p. 56)

4. Underleaves distinctly connate on side nearest adjacent leaf or connate on both sides. New Zealand 10

10. Leaves ± symmetric: the dorsal and ventral margins ± evenly curved or the ventral at most somewhat more arched; leaves bifid to 0.2–0.3, typically subhorizontal, at least in distal sector, never squarrose dorsally; ventral lobe of leaf often larger than the dorsal; underleaves connate on 1 side, obscurely connate or free on the other; shoots larger, to 2 mm wide. Throughout New Zealand; on wood (bark of upright trees + decaying logs) . . . . . *C. lentus* (p. 23)

10. Leaves strongly asymmetrically deltoid, the dorsal-basal sector conspicuously dilated and forming an obvious flange of tissue; leaves bifid to (0.25)0.35–0.55, squarrose dorsally or nearly so; ventral lobe of leaf often smaller than the dorsal; underleaves connate on both sides; shoots smaller, to 0.8 mm wide. New Zealand, South Is.; on rotted wood . . . . *C. herzogii* (p. 59)

Chiloscyphus lentus (Hook. f. & Taylor) J. J. Engel & R. M. Schust.

Jungermannia lenta Hook. f. & Taylor, London J. Bot. 3: 379. 1844. *Lophocolea lenta* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 162. 1845. *Chiloscyphus lentus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 418. 1985 (1984). Type: Auckland Is., Nov. 1840, *Hooker* (BM[5]!–c. per., FH!–c. per.).

Jungermannia diademata Hook. f. & Taylor, London J. Bot. 3: 560. 1844, *syn. fide* Mitten (1854–55). *Lophocolea diademata* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 692. 1847. Lectotype (*nov.*): New Zealand, 1843, *Hooker s.n.* (FH!–c. sporo. + ♂); ?isolectotypes: (BM!–c. sporo. + ♂).

Lophocolea knightii Steph., Bull. Herb. Boissier 6 (10): 879. 1906 (= Spec. Hep. 3: 104), *syn. fide* Hodgson (1953). Type: New Zealand, without specific loc., *Knight 618* (G!–c. sporo. + ♂).

Lophocolea goebeliana Steph., Bull. Herb. Boissier 6 (10): 881. 1906 (= Spec. Hep. 3: 106), *syn. fide* Hodgson (1953). Lectotype (*nov.*): New Zealand, Ins. Meridion (South Is.), Mt. Winterslow, *Beckett 497* (G!–c. per. + ♂).

Lophocolea cheesemanii Steph., Bull. Herb. Boissier 6(10): 882. 1906 (= Spec. Hep. 3: 107), *syn. nov. Chiloscyphus cheesemanii* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 412. 1985 (1984). Type: New Zealand, Auckland, 1895, *Cheeseman 24* (G!–c. per.).

Plants prostrate, often tightly appressed to substrate, the tips at times ascending, the plants pale green; shoots to 2 mm wide. Branches common, of *Frullania* type (the half-leaf undivided or, if bifid, then of similar form to vegetative leaves) or lateral-intercalary type and commonly from ventral-basal sector of stem but variable in position, the two branch types of about equal frequency; ventral-intercalary branches very rare (2 branches seen). Stems narrow for plant size, 7–8 cells high, the cortex rather well differentiated, in a single layer of slightly thick-walled cells, the dorsal and lateral cortical cells distinctly larger than medullary cells, the ventral subequal to medullary cells or slightly larger; medullary cells distinctly thick walled. Rhizoids in loose to tight fascicles from stem at immediate base of underleaves, the tips often branched. Leaves alternate, dorsally assurgent at least in basal sector and sometimes so throughout, widely spreading, loosely imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end and often aligned at an oblique angle toward shoot apex, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells (even in juvenile phases), (the insertions of opposing leaves often extending to the dorsalmost laterally juxtaposed rows of stem cells and not to exact midpoint of stem). Leaves gradually and gently convex, subsymmetrically to symmetrically ovate (often narrowly so and grading to subelliptic) to ovate-trapezoid, widest near base; apex bifid to 0.2–0.3, with lobes ± parallel to slightly diverging, plane, the ventral often larger but not markedly so, the lobes acuminate to subcaudate, the distal sector piliform, terminating in a uniseriate row of 4–11 cells that are wider than long, isodiametric or at most slightly longer than wide and then 14–22 µm wide × 18–28 µm long or 1.1–1.6× longer than wide, the lobe margins entire, the sinus rounded (often broadly so) to lunate; dorsal margin broadly and gently curved, plane, entire, sometimes repand, at most short decurrent; ventral margin broadly and gently curved, at times somewhat more strongly curved than the dorsal, plane, entire, sometimes repand. Leaf cells with trigones minute to small and concave sided to (often) medium and straight sided, median leaf cells 20–30 µm wide, 20–34 µm long; surface smooth or faintly roughened. Oil-bodies hyaline, 5–7 per cell, moderately papillose, elliptic to ± fusiform, some globose, most 8.8–12.7 × 3.9–5.9 µm. Underleaves much smaller than leaves, 1.1–1.5(1.7)× stem width, distinctly but narrowly connate on 1 side and long decurrent and obscurely connate or free on the other, the insertion inverted U-shaped, the underleaves slightly spreading, approximate to contiguous, unistratose, plane to slightly convex (ventral view), obtrapezoid, the apex 2–4-lobed in well-developed phases, 2-lobed in suboptimal plants, the lobes narrowly acuminate to caudate, the median pair normally larger, mostly diverging, sporadically ± parallel, the lateral pair mostly parallel with median lobes, sporadically oriented ca. 90° to stem, the lobes 3–6 (very rarely 7–8) cells wide at base, entire margined (rarely with a tooth on outer margin of median lobe) and terminating in a uniseriate row of 4–8 cells that are wider than long, isodiametric (often) or at most slightly longer than wide and then being 14–24 µm wide × 22–32 µm long or 1.1–1.6(1.8)× longer than wide, the median sinus often V-shaped, descending nearly to underleaf base and delimiting a lamina of only a few cells high (normally 2–4[5]cells), the lateral pair of sinuses of equal depth or (often, especially in suboptimal plants) the median sinus deeper and then the outermost processes appear lateral in position, and the underleaves appear bifid, the lateral processes variable in stature, occasionally reduced and ciliiform, laciniiform, dentiform, or lacking altogether, the apex and lamina margins otherwise lacking other armature.

Asexual reproduction by regeneration; gemmae not seen.

Plants dioecious. Androecia on leading shoots or elongate, indeterminate, lateral-intercalary branches, very rarely on *Frullania*-type branches, the androecia initially terminal but often eventually become intercalary, the male branches sporadically appearing to cease growth, but more often proliferating vegetatively distally (the androecium then basal on a lateral branch); androecia subfolious to subspicate, often composed of numerous (up to 18) bract pairs; bracts somewhat to markedly smaller than leaves, erect, vertical, strongly dorsally assurgent, rather tightly appressed to bract immediately above, the saccate portion smooth to crenulate in profile and fused toward base with opposite bract, the bracts ventricose in basal portion, the distal portion stiffly vertical to slightly reflexed, the apex often similar to leaves in lobe form, at other times the lobes becoming reduced and then medium to wide acute to apiculate to even lacking, the apices then retuse to truncate, the ventral margin of bract entire; lobule margin inflexed to involute, the distal sector with a conspicuous dentiform to acuminate process and often also with 1–2 accessory teeth, one of which is sometimes in the sinus between the dorsal margin of the lobe and the distal tooth of the lobule, the free margin of the lobule otherwise irregularly crenulate to dentate and at times also with an involute acuminate process, the margin at most with 1–2 sessile or stalked slime papillae; antheridia solitary, the stalk long, to 28 cells, uniseriate. Gynoecia on main shoot and lateral-intercalary branches of variable length: grading from abbreviated and without vegetative leaves to long; subfloral innovations frequent, from below bracts of innermost or second series; vestigial stem perigynium absent. Bracts crowded, somewhat *Plagiochila*-like in appearance, transversely oriented, those of innermost series much larger than leaves, suberect to erect and ensheathing perianth base, free from one another, narrowly inserted, distinctly convex, becoming subcanaliculate distally, narrowly ovate; apex bifid to 0.15, the lobes subequal in size or the ventral a little larger, the lobe margins entire; dorsal margin of lamina abruptly deflexed and forming a weak cnemis, entire, the ventral margin abruptly deflexed, entire. Bracteoles of innermost series somewhat smaller than bracts, narrowly connate on 1 side, concave (ventral view), narrowly ovate-elliptic; apex bifid to 0.3, the lobe margins entire; lamina margins entire. Perianth longly exserted beyond bracts, sharply trigonous and prismatic throughout, the sides sometimes somewhat infolded, the perianths long and narrowly oblong, rarely obovate, 3.8–4.4× longer than broad, not to slightly narrowing toward mouth (the degree depending on lobe orientation), deeply 3-lobed, the lobes free for ca. 0.45–0.6 the perianth length; lobes conspicuously and gradually narrowing toward apex, deeply bifid, the segments usually acuminate to caudate, rarely medium acute to short acuminate, entire, the lobes otherwise spinose dentate-laciniate in basal half; keels sharp, with keelar wings common, of a few cells high, mostly entire, occasionally with a laciniiform process.

Seta 6–11 cells in diam., with 15–31 rows of outer cells surrounding an inner core of scattered somewhat to distinctly smaller cells with corners thickened as in minute trigones (a few cells in core center ± equal in size to epidermal cells). Capsule elliptic, the wall 30–42 µm thick, of 3–4 layers, the outer layer of cells subequal to or exceeding thickness of all combined interior strata; outer layer of cells subquadrate to short subrectangular, the radial walls with magenta nodular thickenings which are on some but not all longitudinal walls and only sporadically on transverse walls, the outer wall with weak tendency toward two-phase type of distribution of thickenings (i.e., longitudinal walls with rather dense thickenings alternating with those with few or no thickenings); intermediate and inner layer of cells subequal in thickness or the intermediate layer(s) slightly thicker than inner layer, the intermediate layer(s) with vertical thickenings often tangentially extended; innermost layer of cells irregularly long rectangular, the vertical radial walls with thin continuous sheets of red-brown wall material, with semiannular bands red brown, narrow, often incomplete, rarely forked, the radial walls with nodular to spine-like thickenings often present on both longitudinal and transverse walls.

Spores 11–13 µm, yellow brown, with dense, low but sharply defined, close papillae and short-vermiculate markings; spore:elater diameter ratio 1.3–1.5:1. Elaters tortuous, 7.2–8.2 µm wide, the spirals 2.4 µm wide.

DIFFERENTIATION—This is a primitive member of the genus and one that offers few specialized features to be used taxonomically. The distinguishing features of the species, when well-developed, sterile plants are at hand, include 1) the ± symmetrical, ovate to ovate-trapezoid, uniformly entire-margined leaves that are 0.2–0.3 bifid (Fig. 7: 6, 7); 2) the acuminate to subcaudate lobes that terminate in a uniseriate row of 4–11 cells that are wider than long, isodiametric or at most slightly longer than wide (Fig. 7: 10); 3) the deeply lobed underleaves, the median sinus descending nearly to the underleaf base and delimiting a disc of only a few cells high (Fig. 7: 7, 9); and 4) the conspicuous lateral processes of the underleaf, if optimal then much like the median pair of lobes, the underleaves, are then 4-lobed. Lateral processes of the underleaf are nearly always present, but may be reduced in size, and then laciniiform, ciliiform, dentiform, or, occasionally, in suboptimal or juvenile phases, lacking. The lobe, disc margin, or both may have an accessory tooth, but the basic form of the underleaf is that of two principal lobes and two lateral processes that vary in stature.

Gynoecial plants provide valuable diagnostic characters, even when gynoecia are young. Gynoecial features that are especially useful are the deeply lobed perianths (to 0.6) (Fig. 7: 1, 5); the acuminate to caudate, entire segments (Fig. 7: 1, 5); and the concave, shallowly bilobed, entire-margined bracteoles (Fig. 7: 1, 2).

Useful characters derived from androecial plants are the conspicuous distal tooth on the lobule (Fig. 7: 11, 12); the frequent presence of a tooth in the sinus between the dorsal margin of the lobe and the distal tooth of the lobule (Fig. 7: 11, 12); and the paucity of slime papillae on the lobule margin (Fig. 7: 12).

To gain a full understanding of *C. lentus*, one must also have a concept of juvenile phases of the species. This is particularly relevant because at times, populations consist exclusively, or nearly so, of such plants. To understand the juvenile phase, it was essential to first demonstrate a direct link to well-developed phenotypes of the species. *Schuster 67-3667* was selected because this collection consists, for the most part, of a ± optimal expression of the species (Fig. 7: 3, 6–8, 13). A tertiary branch was examined initially; it had leaves that were distant, elliptic-subrectangular, bifid to ca. 0.3–0.5, 7–8 cells wide, the median cells being 20–25 µm wide × 24–28 µm long, and underleaves bifid nearly to the base and with a disc 1–2 cells high. The branch has an aspect somewhat like a *Telaranea* sect. *Neolepidozia* (Fig. 9: 13). Because the cell number in such leaves is small, the cells appear huge for the leaf size; cell size, however, is within the range exhibited by well-developed leaves. Character expression involving the branch was then compared with a shoot that exhibited precocious production of gynoecia. The shoot consisted of ca. 20 gyres of leaves (Fig. 9: 1, drawn to same scale as Fig. 7: 3, 8), but the characteristics of these leaves are revealing. Those in the distal sector of the shoot were comparable in shape and form to leaves of well-developed shoots. Leaves in the basal sector were more juvenile in aspect and were comparable to those of the tertiary branch (compare Fig. 9: 10 with 13), although they may be somewhat wider (to 10 cells in diam.). Cell size also is comparable, here being 20–25 µm wide × 24–28 µm long. Leaves in the median sector of the shoot were ± intermediate (Fig. 9: 9).

The nature of the juvenile phase was also assessed via a second, more direct and positive link. Numerous tiny shoots, variable in size, were intermixed with adult phases of plants in *Schuster 67-3667*. The larger ones were unattached and interwoven among the adult, optimal phases. However, in many instances, it was possible to establish a direct physical connection of smaller shoot to parent plant as a result of regeneration. Regeneration was common from the inner face of the perianth (Fig. 9: 8). These regenerants possessed the features outlined above for the tertiary branch. (The leaf cells of the regenerant, however, were somewhat smaller than those of the tertiary branch, being 20–26 µm wide and long, but still within the range for the species.) The rather copious tiny shoots in the population, then, were probably all or mostly due to regeneration. Regenerant leaves possess several characteristics of the adult plant within a relatively small number of gyres. For example, leaf cells may possess distinct trigones (Fig. 9: 11) and have cells similar in size to those of mature shoots.

As mentioned above, some populations consist predominantly of the juvenile phase; examples are *Engel 18756* and *18758*. Smaller shoots of such populations are comparable to the juvenile plants intermixed with the well-developed plants, as in *Schuster 67-3667*, and to the regenerants. The cell size of such plants (e.g., *Engel 18756*) also fits within the range of the species, although they are in the smaller part of the size range, being 22–25 µm wide and long. Gradations from juvenile to well-developed shoots are usually demonstrable within a population; several shoot sectors of *Engel 18758* were illustrated to depict this (Fig. 9: 2–6). The extent of leaf insertion dorsally remains a valuable character in juvenile phases. Like well-developed phases, insertions of opposing leaves extend either to the stem midline dorsally or to the dorsalmost pair of laterally juxtaposed rows of stem cells (Fig. 9: 10, 11, 13). Substrate should also be considered when working with juvenile phases because such plants are nearly always, like the optimal phase, corticolous.

Special care is required in separating *C. lentus* from suboptimal *C. subporosus* (see Table 6 under that species, p. 42). The two species may be distinguished by the following key.

Key to *C. lentus* and *C. subporosus*

1. Leaf cells not dimorphic, no scattered enlarged cells; underleaves distinctly but narrowly connate on 1 side; terminal and lateral-intercalary branches both common; trigones often medium; leaves ± symmetric: the dorsal and ventral margins ± evenly curved or the ventral at most somewhat more arched; leaves, at most, short decurrent dorsally; leaf border lacking; underleaf lamina 2–4 cells high; perianths commonly produced; ♀ bracteoles connate on 1 side . . . . *C. lentus*

1. Leaf cells dimorphic: enlarged cells scattered among smaller cells; underleaves nearly always uniformly free (sporadic suboptimal populations aside); terminal branches predominant, lateral-intercalary branching rare; trigones minute to small or absent; leaves distinctly asymmetric (well-developed plants):

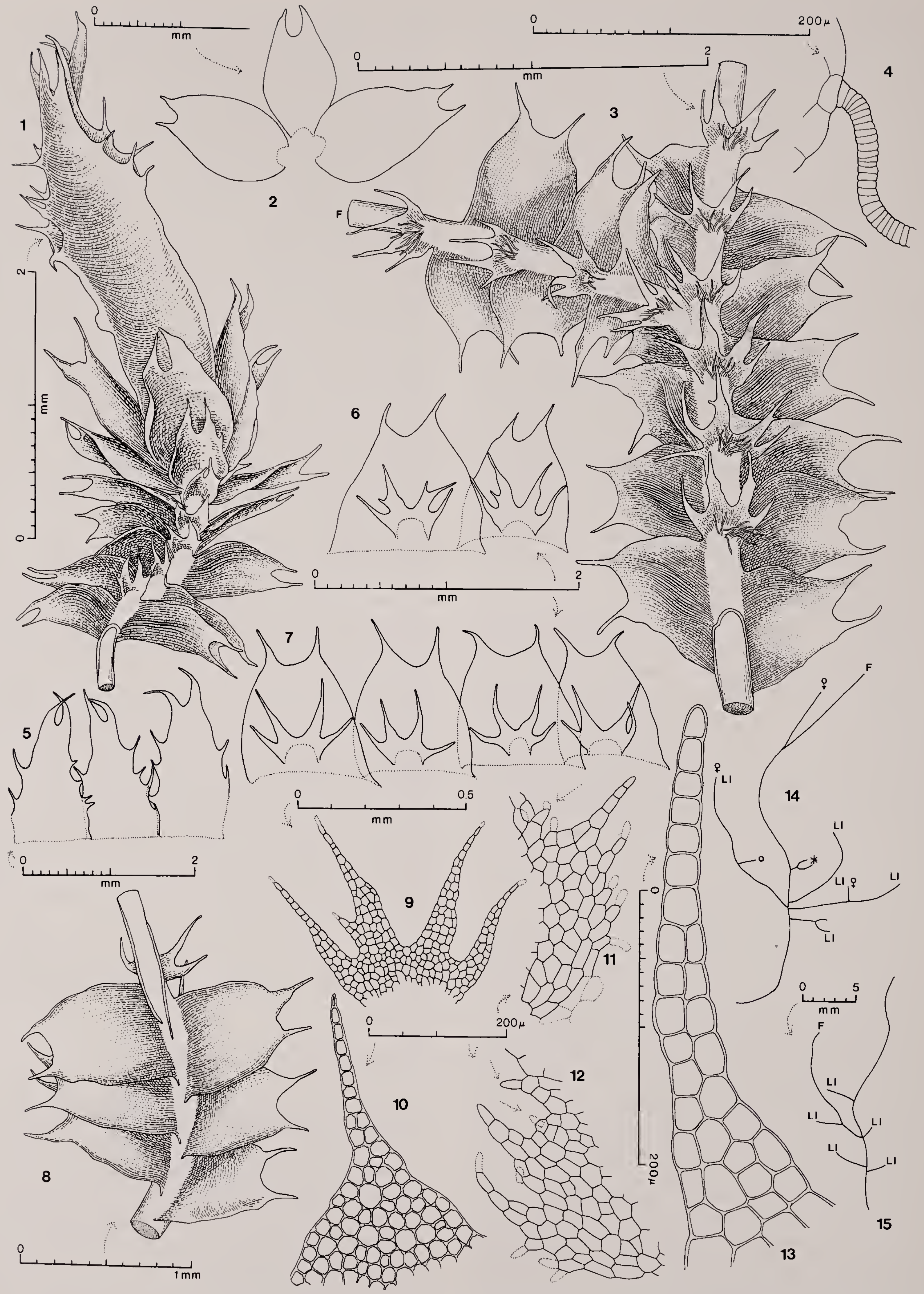


FIG. 7. *Chiloscyphus lentus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **1.** Gynoecium, ventral view. **2.** ♀ Bracts and in middle, bracteole (note that figure is drawn at 50% smaller than leaves and underleaves in **6** and **7**). **3.** Sector of main shoot with *Frullania*-type branch (= F; note form of first branch leaf), ventral view. **4.** Antheridium. **5.** Perianth mouth, ventral lobe in middle. **6, 7.** Leaves and within, underleaves, at same scale (those in **6** all from same shoot; those in **7** all from a second shoot). **8.** Sector of main shoot, dorsal view. **9.** Underleaf. **10.** Segment of leaf. **11, 12.** Male bract margins (2 from same shoot), note teeth (at arrows) in sinus between lobe and lobule; note also variation in armature. **13.** Segment (complete) of underleaf. **14.** Cladograph of plant with exserted but young perianths (= U-shaped symbol, that with an asterisk [*] = gynoecial branch lacking vegetative leaves) as well as gynoecia with perianths not yet exserted (= O); F = *Frullania*-type branch; LI =

TABLE 3. Comparison between *Chiloscyphus lentus* and *C. latifolius*.

Character	*C. latifolius*[1]	*C. lentus*
Shoot width (mm)	(2)2.5–3	1–2
Branching frequency	sparing	common
Branch type	most often terminal	terminal and lateral intercalary both common
No. of cells in uniseriate row of leaf lobes	1–5	4–11
Cells in uniseriate row of leaf lobes	± elongate (cf. Schuster, 1980, fig. 521: 13, p. 196)	wider than long, isodiametric, or at most slightly elongate
3-Lobed leaf frequency	potential, isolated	lacking
Trigones	lacking	often medium
Underleaf lamina height	demonstrable (cf. Schuster 1980, fig. 521: 14, p. 196)	reduced, 2–4 cells high
♂ Bract apex	2–3-lobed	2-lobed, the lobes may be reduced or lacking
Perianth frequency	rare	common
Perianth lobe segments	broadly triangular acuminate	acuminate to caudate

[1] All data on *C. latifolius* obtained from Schuster (1980).

the dorsal margin straight or curved inward and lunate, the ventral distinctly and broadly arched; leaves long decurrent dorsally; leaf border of large cells often weakly to distinctly developed; underleaf lamina 5–11 cells high in well-developed plants, 2–4 cells high suboptimally; perianths rarely produced; ♀ bracteoles free . . . . *C. subporosus*

This species is an ally of *C. latifolius* (Nees) J. J. Engel & R. M. Schust. (= *Lophocolea bidentata* (L.) Dumort.), and an underleaf-free species that also may occur on wood; the species has a north temperate range and is particularly common in Europe. The two species, while strikingly similar in aspect, differ by a number of features, several of them rather subtle. The two species are contrasted in Table 3.

VARIATION—Well-developed plants have both leaf and androecial bract apices distinctly bifid by lobes that are subcaudate. However, the lobes of ♂ bracts may at times have lobes that vary from medium or wide acute to apiculate to merely retuse to truncate. Examples of lobe reduction or loss are *Hatcher 792* and *937*.

Suboptimal perianths (ex. *Hatcher 126*) differ from well-developed, typical ones being short and clavate, to campanulate, obscurely trigonous, less deeply lobed, and with segments less extended, being acuminate.

NOTES—1) Lateral-intercalary vegetative and sexual branches usually issue from the ventral-basal sector of the shoot in the vicinity of leaf–underleaf connation. Other positions, however, are common. Branches may be ventral-lateral and ± midway between two underleaves; the branch is then basal to the median sector of a leaf or even basal to the insertion of an underleaf. At other times, the branch appears closer to an underleaf and then appears in the lateral half of an underleaf axil. True ventral-intercalary branches (from the median sector of the underleaf axil) are very rare. Lateral-intercalary branches are often short and small in relation to the parent shoot and consist of a few gyres of small leaves.

2) Most Rodway-determined specimens labeled *Lophocolea lenta* are actually either *C. perpusillus* or *C. subporosus*.

NOTES ON TYPE SPECIMENS—1) *Jungermannia lenta* Hook. f. & Taylor. The specimen at FH is rather copious; a few perianths are present, but no sporophytes. Evidence of a bark substrate is lacking, but Taylor and Hooker (1845, p. 154) stated that the species occurred "in large tufts upon the moist trunks of trees." I have seen only lateral-intercalary branching. Leaves are ± symmetrically ovate (Fig. 8: 8–10), and the lobes terminate in a uniseriate row of (4)5–6 cells that are often wider than long or isodiametric (Fig. 8: 5). The lobes are rather variable and not attenuated as in other populations (compare lobes in Fig. 8 with those in Fig. 7); a minority of lobes are merely medium acute and terminate in a single cell (Fig. 8: 4) or ± apiculate. The surface is faintly roughened (Fig. 8: 2). Underleaves are small for the shoot size, distinctly but narrowly connate on 1 side, and free or feebly connate on the other (Fig. 8: 1). The underleaf lamina is 2–3(4) cells high (Fig. 8: 3), and margins are entire or have a tooth on one or both sides (Fig. 8: 1, 3). Perianths deviate somewhat from the optimal condition. They moderately expand toward the mouth (the "calyx" is described in the protologue as "obovato"), have acuminate segments, and are somewhat exserted beyond the bracts (suggesting that the gynoecium is immature). Optimal, mature gynoecia are long, narrowly oblong (without expansion toward the mouth), have acuminate to caudate segments, and are longly exserted beyond bracts (Fig. 7: 1, 5; Mitten, 1854–55, pl. 97, fig. 4).

Because the type consists of immature gynoecia, a question arises as to origin of the capsule in the protologue. I could not answer the question definitively, although some information may be obtained from nonprotologue sources. A year after the species was published, Taylor and Hooker (1845), as in the protologue, included capsule-bearing plants in their description and commented (p. 154) that "this species will be figured in the Flora of New Zealand, of which island also it is a native." The figures of the species in Mitten (1854–55) include both dehisced and nondehisced capsules on elongated setae. Mitten cited two collections for the species: one from North

←

lateral-intercalary branch. **15.** Cladograph of sterile plant (symbols for branch types the same as in **14**). (**1, 2, 5,** from *Schuster 67-981*, New Zealand, North Is., Manginangina Reserve; **3, 6–15,** from *Schuster 67-3667A*, New Zealand, North Is., Coromandel Peninsula; **4,** from *Hatcher 1276*, New Zealand, North Is., Wairoa.)

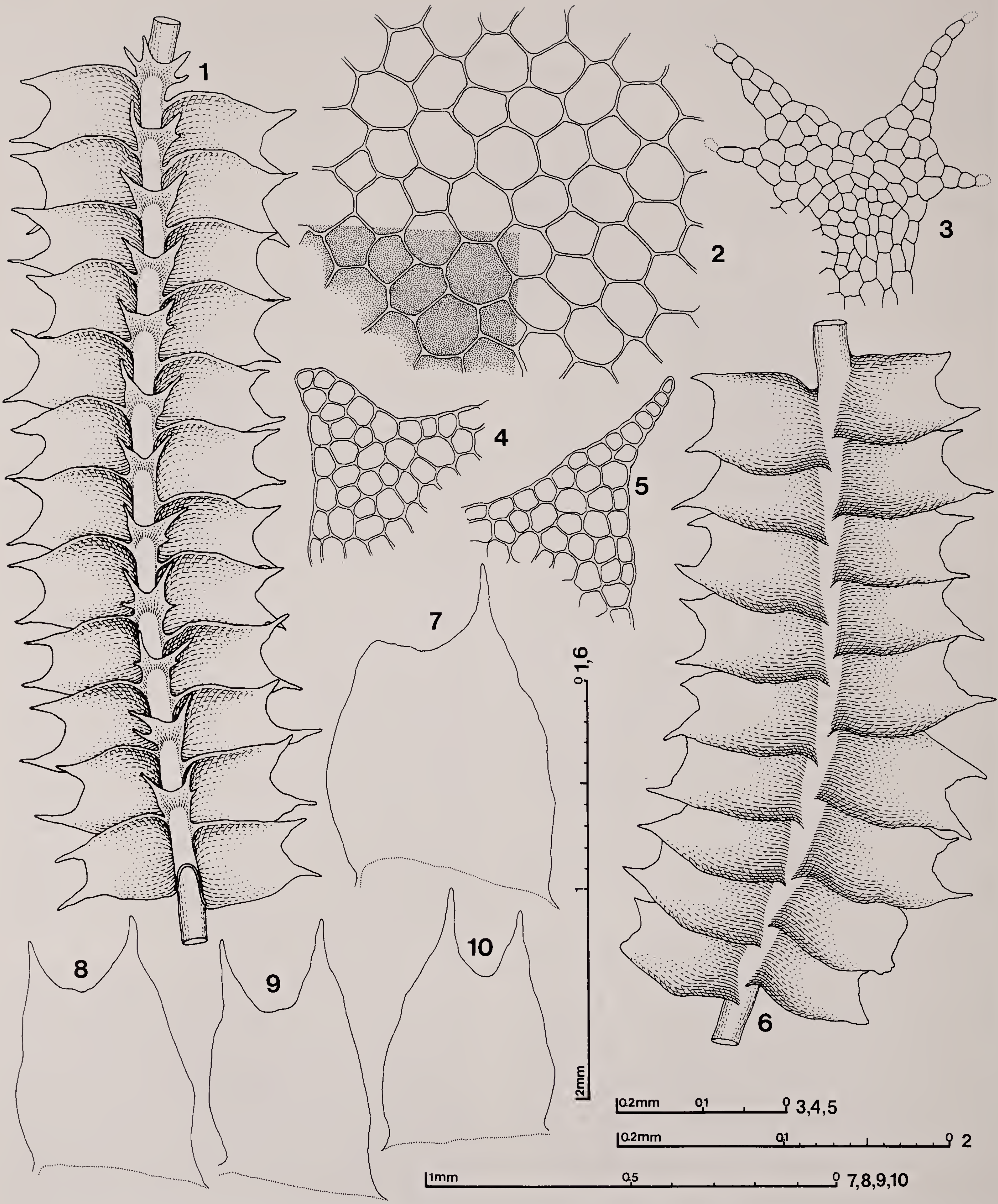


FIG. 8. *Chiloscyphus lentus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **1.** Main shoot, ventral view. **2.** Median leaf cells; stippled portion indicates roughened cuticle. **3.** Underleaf and adjacent stem cells. **4, 5.** Leaf segments. **6.** Main shoot, dorsal view. **7–10.** Leaves. (All from type material of *Jungermannia lentus* [FH].)

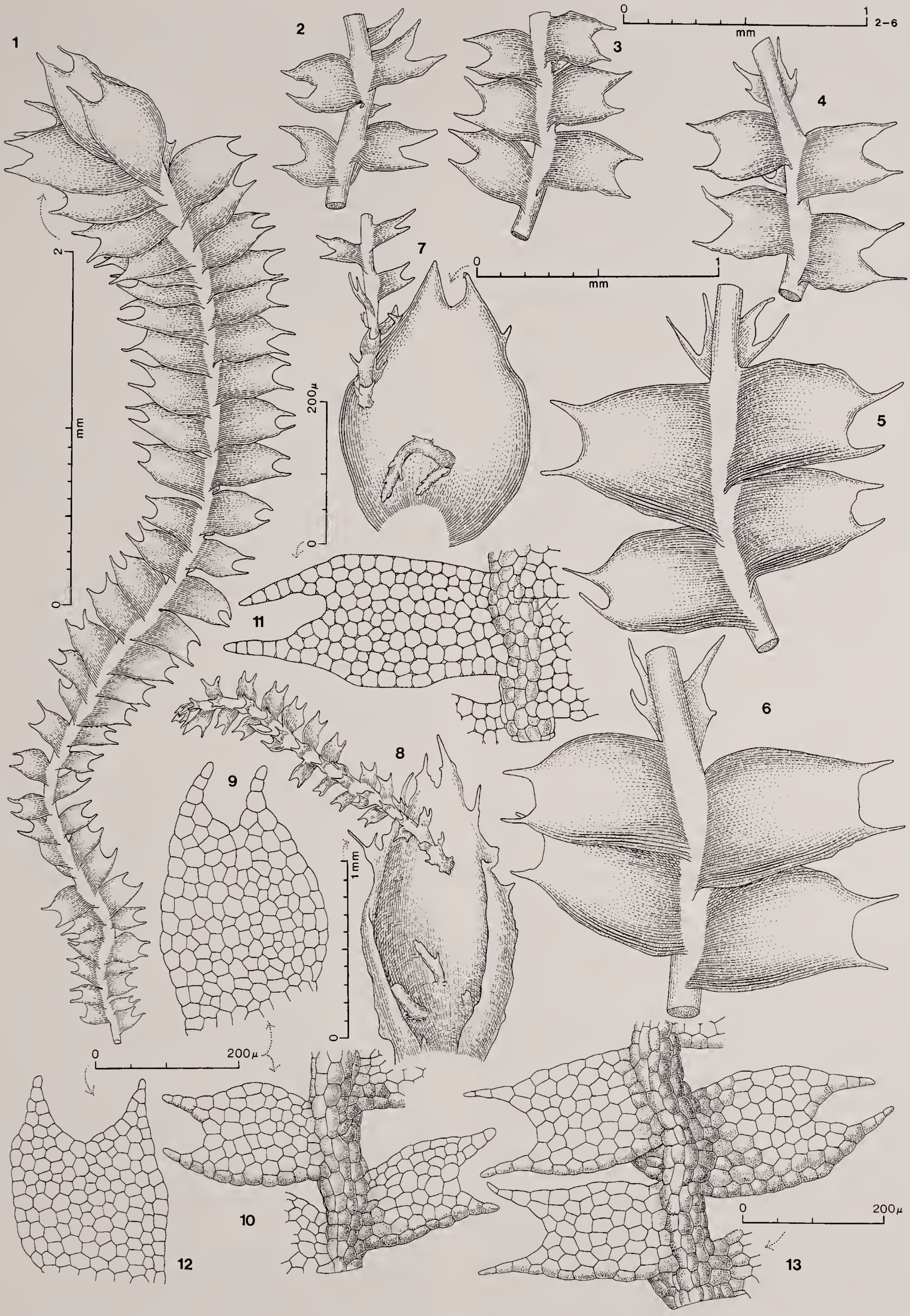


FIG. 9. *Chiloscyphus lentus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **1.** Shoot showing precocious production of gynoecium (flattened), the leaves in distal sector somewhat like those of well-developed shoots, the leaves in median sector somewhat more juvenile in aspect (see 9), those toward base of shoot with juvenile aspect (see **10**). **2–6.** Series of 5 shoot sectors to illustrate intra-population variation ranging from juvenile to rather well-developed phases. **7.** Leaf with three regenerants. **8.** Inner face of perianth showing various stages of regeneration. **9.** Leaf (from median sector of shoot in **1**). **10.** Opposing leaf pair from sector ca. 9 gyres (from base of shoot in **1**). **11.** Sector of regenerant from inner face of perianth. **12.** Leaf of juvenile phase. **13.** Sector of tertiary branch. (**1, 7–11, 13,** from *Schuster 67-3667A*, New Zealand, North Is., Coromandel Peninsula; **2–6, 12,** from *Engel 18758*, New Zealand, South Is., Fiordland Natl. Park, track along East Branch of Eglinton River.)

Is., Bay of Islands, leg. Hooker, the other a Colenso plant from Wairarapa valley (East Coast). An 1843 Hooker collection at FH from New Zealand (unfortunately without specific locality) bears both dehisced and nondehisced capsules on elongated setae. That collection may have been the source of capsule-bearing plants referred to in the protologue.

2) *Jungermannia diademata* Hook. f. & Taylor. The protologue of this species does not include collector, but does state that "perigonia" (androecia) as well as both dehisced and nondehisced capsules are present. Candidates for lectotype at FH include a specimen collected by Hooker and one by Colenso. (Collections at BM have fragmentary label information that is insufficient for purposes of lectotypification.) Several points support selection of the Hooker specimen. First, the collection has androecia as well as dehisced and nondehisced capsules. Second, the underleaf lamina on each side has a prominent lacinium, thus agreeing with the protologue, which states underleaves are quadrifid. Third, the Hooker specimens are mounted on a small sheet on which are illustrated bracts and bracteole *in situ*, a ventral view of a shoot sector, and 2 views of a perianth. These figures closely match the description. The Colenso specimen, on the other hand, has dehisced capsules but no indication of androecia. Furthermore, underleaves have lamina margins predominantly entire and only sporadically have a process. I have designated the Hooker specimen as lectotype.

The lectotype represents a rather well-developed phase of *C. lentus*. The uniseriate row of the leaf lobes is composed of 4–6 cells, the perianths are elongate and resemble that shown in Fig. 7: 1, 5, and the underleaves are distinctly but narrowly connate on 1 side. The specimen occurred on wood and is mixed with *Frullania* sp. and a moss (Hypnaceae). Two probable isolectotypes are at BM, but without collector.

3) *Lophocolea knightii* Steph. The specimen is a small phase of *C. lentus* and consists of shoots with androecia, perianths, and abundant, mostly dehisced capsules; of these, only perianths are noted in the protologue. Nearly all shoots are fertile. Stephani states that the plant is corticolous, but this is not clear from the specimen. The strongly dorsally assurgent leaves have lobes with a uniseriate row consisting of (3)4(5) cells, thus being a low extreme for *C. lentus*. The underleaves are distinctly narrowly connate on 1 side, and the lamina on each side has a dentiform process. Trigones are medium and straight sided and not "parvis" as stated in the protologue. The perianth deviates from those of optimal *C. lentus* in being obovate, not as deeply trilobed, and with lobes medium acute to short acuminate to at most moderately acuminate. This armature lends the perianth mouth a spinose appearance quite unlike the usual condition (shown in Fig. 7: 1, 5). See comments sub Variation.

4) *Lophocolea goebeliana* Steph. The protologue states "typus in herb. Stephani," cites Beckett and Cheeseman as collectors for "Ins. meridion" (South Is.), New Zealand, and includes a description of both gynoecia and androecia. Three specimens bearing this name are at G:

a) *Beckett 395* from Akaroa, Banks Peninsula (South Is.). This specimen does not have perianths or androecia and therefore significantly deviates from the protologue. It is *C. lentus*.

b) *Beckett 497* from Mt. Winterslow (South Is., 43°35′S, 171°24′E). Most shoots of this specimen are androecial or gynoecial; few sterile shoots are present. The specimen agrees well with the protologue except in a few respects: underleaves are often connate on 1 side (in the protologue leaves are said to be free), and trigones are small to medium and not "magnis acutis." The Stephani icon of this species (*Lophocolea* no. 127) is based on Beckett material from "Insa. meridion," and because a figure of a perianth is included, the icon (of at least the perianth) is based on *Beckett 497*. I have designated this specimen as lectotype. The specimen represents a somewhat suboptimal phase of *C. lentus*.

c) *Cheeseman 21* from Auckland (North Is.). The specimen has no perianths and the collection site deviates from the protologue. The collection represents a rather vigorous phase of *C. lentus*.

This is an exceptional case of eponymy in which Stephani named a species after an individual who did not collect the original material.

5) *Lophocolea cheesemanii* Steph. Underleaves are divided nearly to the base, the lamina being only ca. 2 cells high. The underleaves are not bifid to 0.5 as mentioned in the protologue and illustrated in the Stephani icones (*Lophocolea* no. 122). Underleaves are typically narrowly connate on one side. However, this character is not uniformly expressed, in that some shoots have sectors with free underleaves. Leaves are subsymmetrically rather narrowly ovate and have lobes with a uniseriate row of to 7 cells. Trigones are small. Perianths are immature and interestingly have a broad spectrum of wing development (even on a single perianth), ranging from relatively high and fringed with well-developed laciniae to short and then with or without teeth keels that are wingless. The perianth summit is similar to Fig. 7: 1. The substrate is clearly bark.

DISTRIBUTION—I previously regarded this species as having an amphipacific distribution, occurring rather widespread in subantarctic and south temperate areas (Engel, 1978, 1990a). After study of the genus in Australasia, including the type of *C. lentus*, I am confining the range of the species to New Zealand (Stewart Is., South Is., North Is.) and its offshore islands (Campbell, Auckland, and Snares Is.). Specimens reported from Tasmania are misdeterminations, mostly of *C. subporosus*.

ECOLOGY—The plant is a common forest species in New Zealand at low to medium elevations—typically 15–520 m on South Is. and sea level to 760 m on North Is. I have seen only a few specimens from elevations higher than the above. For example, ca. 1280–1390 m on South Is. in a *Nothofagus fusca–N. solandri* forest (Pinchgut Track, Nelson Lakes Natl. Park, *Engel 21415*). The species is particularly common on old, decayed logs, bark of living and dead trees, trunks of shrubs, and, to a lesser extent, on tree fern trunks. A partial shift in substrate occurs at the southern extremity of its range (Campbell, Auckland, and Stewart Is.), where the species may be terricolous. A nonwoody substrate is exceedingly rare on North and South Islands.

SPECIMENS SEEN (selected)—**CAMPBELL IS.:** *Oliver s.n.* (CHR). **AUCKLAND IS.:** *Erebus & Terror Exped.* (BM); *Oliver H 15* as *L. perpusilla* (CHR); Ewing Is., *Fineran 1440* (CHR). **NEW ZEALAND.** Without specific loc., *Colenso s.n.*–c. sporo. (FH); ibid., *Hooker s.n.*–c. sporo. + ♂ (FH). **STEWART IS.:** Stage Is., one of the Mutton Bird Islands near Stewart Is., *Fineran 18* (CHR); Paterson's Inlet, Ulva Is., *Hatcher 1616*–c. per. + ♂ (F, UWM); between Half Moon Bay and Deep Bay, *Hatcher 1576* (F, UWM); Fern Gully Track at terminus of Kaipipi Road, Mill Creek, ca. 2 km W of Oban, 20–30 m, *Engel, von*

Konrat & Braggins 24069 (F); Ulva Island, Paterson Inlet, sea level to ca. 60 m, *Engel, von Konrat & Braggins 24611* (F). **SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, off track along E Branch of Eglinton River, SE of Mt. Eglinton and NNE of Te Anau, 440 m, *Engel 18756, 18758* (F). **OTAGO:** Berwick State Forest, S of Dunedin, ca. 60 m, *Allison H 1362* (CHR); Waipori Gorge, S of Dunedin, *Allison H 1356* (CHR); Morrison's Creek, N of Dunedin, 330 m, *Engel 17693*–c. ♂ (F); Lee Stream, Hindon Road, ca. 305 m, *Child H 899* as *L. bispinosa*, *H 901* (F); Paradise, Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, *Child H 1249* (F); Paradise, Jordan River, head of Lake Wakatipu, ca. 520 m, *Child H 2482* as *L. bispinosa* (F); Route Burn Valley, ca. 520 m, *Child H 2434* as *L. bidentata* (F); Fiordland Natl. Park, Martin's Bay, N of McKerrow River, *Hatcher 792, 937*–c. per. + ♂ (F, UWM). **WESTLAND:** Near Lake Paringa, ca. 15 m, *Child 2493* (BM). **CANTERBURY:** Waimate, *Beckett 241* (G); Bank's Peninsula, Price's Valley, ca. 60 m, *Macmillan 79/251* (CHR); ibid., Kaituna Valley, *Hatcher 99*–c. sporo. + ♂ (F), *128* (F, UWM). **NELSON:** Nelson Lakes Natl. Park, Pinchgut Track, W of southern sector of Lake Rotoiti, SSW of St. Arnaud, ca. 1280–1390 m, *Engel 21415*-c. sporo. + ♂ (F). **NORTH ISLAND. WELLINGTON:** Carter's Bush, Wairarapa, *Braggins s.n.* (AKU); McKenzie Trust Reserve, Nga Manu Sanctuary near Waikanae, *Mues NZ 48* (F); Mt. Marima, ca. 185 m, *Zotov s.n.* (CHR); Taurewa, W of old Ketetahi mill, *Braggins H 72*–c. sporo. (AK). **HAWKE'S BAY:** McKinnon's Bush, near Wairoa, *Hodgson 7* (CHR); near Wairoa, *Hatcher 1855* (F), *1267, 1268, 1854* as *L. bidentata*–c. ♂ (F, UWM); Wairoa, "Kiwi," *Hodgson 42* (CHR); Morere, *Hatcher 87* (F, UWM). **SOUTH AUCKLAND:** Roto-a-kui Bush, E of Taupo, 760 m, *Allison H 3362, H3490* as *L. bidentata* (CHR); E of Taupo, ca. 760 m, *Allison H 3519* (CHR); Puaiti Bush, S of Rotorua, *Allison H 3553* as *L. bidentata*–c. sporo. (CHR); Rotorua, *Lloyd 16* (CHR); ibid., 6 mi. past Okere, *Child 35* as *L. bispinosa* (F); slopes of Moerangi Hill, above Lake Tikitapu (Blue Lake), Rotorua region, *Allison H 3427* (CHR); Kinleith Forest, Tokoroa, *Braggins s.n.* (AK); between Lake Rotoehu and the coast, Bay of Plenty, *Allison H 3340, H 3348* (CHR); Rotoehu Forest, Bay of Plenty, near Pongakawa, *Allison H 3431* (CHR); Dunphail, *Petrie s.n.*–c. sporo. (CHR); ibid., Te Akatea, *Petrie s.n.* (CHR); W side of Coromandel Peninsula, Kauri Clump Forest Reserve, ca. 185–245 m, *Schuster 67-3667A*–c. per. + ♂, *67-3680A* (F). **NORTH AUCKLAND:** Anawhata, *Braggins s.n.* (AK); Orakei, Auckland, *Langridge 177, 205* (AK, CHR); Waitakere Range, Spraggs Bush, *Braggins s.n.* (AK); Waitakere, ca. 150 m, *Child H 2232* as *L. novaezeelandiae* (F); Auckland, Kepa Road Reserve, *Idoine s.n.* (AK); ibid., Te Whau, *Kirk s.n.* (CHR); Rangitoto Is., 50–160 m, *Engel 20784* (F); ibid., Waitamata Harbour, *L.B.M. 32* (CHR); Pohuehue Scenic Reserve, N of Auckland on State Highway 1, ca. 25 m, *Engel 21174* (F); Greenhithe, *Braggins s.n.* (AK); Woodhill, S Kaipora Heads, N of Auckland, *Robbins 6* (AK–c. ♂, CHR); Hen and Chickens Is., Lady Alice Is., 5 m, *Beever 8-73a* (AK); ibid., Whatupuke Is., above Starfish Bay, 120–200 m, *Beever 8-63c, 8-566* (AK); track to Ti Point Scenic Reserve, N head of Whangateau Harbour, S of Leigh, edge of sea, *Engel 20294* (F); Logues Bush Scenic Reserve, 6 km NE of Wellsford, ca. 40–80 m, *Engel 20318* (F); N facing slope W of Bream Head, SE of Whangarei, 290–345 m, *Engel 22285*–c. per. + ♂ (F); summit area of Mt. Manaia, NW of Bream Head, SE of Whangarei, 390 m, *Engel 22225* (F); Waipoua Forest area, *Allison H 749* (CHR); Waipoua River, main road bridge, ca. 245 m, *Child H 2165* as *L. bispinosa* (F); Manginangina Reserve, Puketi Kauri Forest, S of Kaeo, *Schuster 67-981, 67-989A*–c. per. (F); North Cape, Whiriwhiri Stream, *Beever s.n.* (AK); Radar Bush, WSW of Cape Reinga, S of Mt. Te Paki, ca. 100 m, *Engel 20855*–c. per. + ♂ (F). **LITTLE BARRIER IS.:** *Braggins 84/132a, 84/133* (AK); Track 2, SW region, 105–305 m, *Braggins et al. 80/276, 80/305* (AK); Thumb Track, 30 m, *Braggins et al. 80/1010, 80/1034* as *L. bidentata*, *80/1041* as *L. bidentata* (AK); above junction of Track 1 and Thumb Track, 365 m, *Braggins et al. 80/182c*–c. per., *80/182e* (AK); mouth of Waipawa Stream, *Braggins 84/274*–c. per. (AK); mouth of Parihakoakoa Stream, *Braggins et al. 80/33, 80/50* (AK); Te Titoki Point, under Pohutukawa, *Braggins et al. 80/990a* as *L. bidentata*–c. ♂ (AK); N of Te Titoki Point, *Braggins et al. 80/16, 80/23, 80/31* (AK); East Cape Hut., *Braggins et al. 80/333* as *L. bidentata*, *80/340*–c. ♂, *80/342b* as *L. bidentata*, *80/347, 80/377* (AK). **SNARES IS.:** SE promontory, *Fineran 28pp* (CHR); Comma Bay, *Horning 189* as *L. bidentata* (CHR). **CHATHAM IS.:** Crispans Lane, Orihou Stream, ca. 10 m, *de Lange CH1042* (AK, F).

Chiloscyphus bispinosus (Hook. f. & Taylor) J. J. Engel & R. M. Schust.

Jungermannia bispinosa Hook. f. & Taylor, London J. Bot. 3: 378. 1844. *Lophocolea bispinosa* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 162. 1845. *Chiloscyphus bispinosus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 411. 1985 (1984). Type: Campbell Is., *Hooker* (BM!, FH!, S![3]).

Lophocolea mittenii Steph., Bull. Herb. Boissier 6(10): 883. 1906 (= Spec. Hep. 3: 108), *syn. fide* Hodgson (1953). Type: New Zealand, without specific loc., "sub *Lophoc. spinifera* Taylor," *Colenso s.n.* (G!).

Lophocolea minuta Pearson, Univ. Calif. Publ. Bot. 10: 376. *pl. 106.* 1923, *syn. fide* Hodgson (1953). Holotype: New Zealand, North Is., Taupo, May 16, 1904, *Setchell 48*. (UC no. 213702!–c. per.).

Lophocolea curvifolia Herzog, Trans. & Proc. Roy. Soc. New Zealand 65: 353. 1935, *syn. fide* Hodgson (1953). Type: New Zealand, South Is., Marlborough, 1929, *McMahon s.n.* (CHR!, JE!–c. per.).

Plants soft, often with a spiny, *Chandonanthus*-like aspect, loosely creeping to ascending to erect, tending to be notably loose and weft-like, in small tufts, exceptionally in thick, pure, dense carpets, the plants pale yellow green to bright light or pale green; shoots variable in size: ranging from small, thread-like and 0.75–1.8 mm wide to large and 2–3.2 mm wide. Branches very common, in some populations nearly exclusively of *Frullania* type, with lateral-intercalary branches rare, in other populations *Frullania*- and lateral-intercalary–type branches both common, with the latter more predominant; ventral-intercalary branches sporadic; lateral-intercalary branches situated between lateral base of underleaf and ventral base of adjacent leaf or in lateral half of underleaf axil; half-leaf of terminal branches undivided, the apex narrowly acute to subcaudate to piliform or, if bifid, then with the dorsal lobe variable in stature and often a lanceolate process. Stems 11–12 cells high, the cortex poorly differentiated, in 1–2 layers of cells somewhat smaller than those of the medulla, the stem cell walls slightly thickened. Rhizoids from stem at immediate base of underleaf. Leaves alternate, the orientation variable: often grading from subhorizontal to subvertical on same shoot, obliquely to widely spreading, distant to loosely imbricate, free dorsally, orientation strongly succubous or at times subtransverse in smaller phases, the insertion strongly recurved at ventral end (distinctly J-shaped), the lines of insertion extending to (or nearly to) stem midline dorsally and either without a leaf-free strip of stem cells or with a strip 1 cell wide. Leaves broadly convex, in smaller phases usually 220–650 μm wide, ± symmetric, oblong-ovate to oblong rectangular to cuneate, 1.3–2.5× longer than wide, mostly widest in median or distal third; larger phases with leaves mostly 800–2000 μm wide, distinctly asymmetric, short- and wide-subrectangular to wide ovate to trapezoid, 0.75–1.2(1.4)× longer than wide, uniformly widest near the base; apex bifid to (0.35)0.4–0.55(0.6), the lobes variously oriented but often parallel, plane to somewhat ventrally sulcate, subequal or the dorsal larger, long acuminate to (more often) subcaudate-caudate, the tip piliform, consisting of a uniseriate row of 4–11 cells, the lobe margins entire or occasionally 1–2-ciliate or laciniate toward base, the sinus variable, rounded to angular; dorsal margin mostly straight to gently curved inward, less often broadly, symmetrically and gently rounded, plane to somewhat deflexed, entire or with 1–2 cilia or laciniae, not to very long decurrent; ventral margin slightly to moderately rounded to asymmetrically broadly rounded, often sharply curved toward base, sharply and abruptly reflexed, entire or with 1–3 cilia or small to large laciniae. Lobes and at least the distal portion of lamina bordered by 1 or sometimes locally 2 rows of enlarged cells that are often convex at the free face, rendering the margin crenulate. Leaf cells often feebly to distinctly dimorphic (particularly in robust phases): most small, but scattered throughout leaf are conspicuously enlarged cells lending the leaf a speckled appearance; walls thin to slightly thickened, trigones in some populations small and concave sided to medium and straight sided, in others medium to large and slightly bulging, rarely bulging and knot-like, the median leaf cells 13–26 µm wide, 16–30 µm long; surface smooth. Oil-bodies throughout leaf except distalmost cells of lobe, occupying a fraction of cell volume, hyaline or very pale smoky grey, 2 or 2–3(4) per cell or in some populations 3–5 per cell (the large border cells with 2–3[4] per cell), finely to coarsely papillose, ovoid to elliptic to fusiform, most 3.5–6 × 3.2–3.5 µm to 5.9–8.5 × 3.3–3.9 µm, some 7.8 × 4.6 µm, exceptionally 9–11 × 4 µm. Underleaves somewhat smaller than leaves, 1.3–2.8× stem width, free, insertion a- or symmetric, crescent to inverted U-shaped, the underleaves somewhat to rather strongly spreading, distant to contiguous, narrowly ovate to subrectangular to subcuneate, 2–4-lobed, the median sinus descending to near base of underleaf and delimiting a lamina of only 2–4 cells high, the median pair of lobes always larger, the lateral armature variable in stature: sometimes lobe-like (the underleaves then 4-lobed), at times nearly equaling the median lobes in size, sometimes tooth-like to laciniiform (particularly in smaller phases, the underleaves then clearly bifid), the median lobes 3–9 to 13–20 cells wide at base, long acuminate to caudate, the tip piliform and consisting of a uniseriate row of 3–7 cells that are moderately to distinctly longer than wide, the lobe margins reflexed (the lobes ventrally sulcate), with a few often opposing cilia or laciniae or entire; lamina margins reflexed, often with accessory cilia or laciniae in larger phases but entire in smaller ones, long decurrent. Underleaf lobes bordered by a row of enlarged cells.

Asexual reproduction absent.

Plants dioecious, often sterile. Androecia nearly exclusively on main shoot or rather short to long *Frullania*-type branches that are initially terminal but eventually become intercalary, the androecia only sporadically on elongate lateral-intercalary branches; androecia slenderly spicate; bracts somewhat smaller than leaves, obliquely spreading, strongly dorsally assurgent and subvertical, loosely appressed to bract immediately above, the saccate portion fused toward base with opposite bract, the bracts ventricose in basal half, the distal portion plane to broadly reflexed, the apex basically like the leaves except the dorsal lobe is sometimes absent or reduced to a low rounded projection; ventral margin entire or fringed with several short cilia near base; lobule rather large for bract size, the margin inflexed, crowded with numerous ciliiform and often laciniiform processes; antheridia large for bract size, 1(2–3) per bract, the stalk 1-seriate but sometimes with a few local oblique walls. Gynoecia infrequent, on main shoot and short to rather long lateral- and ventral-intercalary branches. Bracts of innermost series much larger than leaves, erect and ensheathing perianth throughout or appressed basally but with the lobes reflexed, the bracts free from one another, convex (dorsal view), narrowly ovate to elliptic; apex bifid to 0.5, the lobes acuminate to subcaudate, ventrally sulcate, entire, or with a cilium near the base; lamina margins reflexed at least distally, the reflexed portions confluent with those of lobe margins, the lamina margins with a few spinose teeth or with a prominent acuminate to subulate appendage at the extreme base of 1 or both sides, or entire. Bracteoles of innermost series similar to bracts in form but somewhat smaller, free from bracts. Perianth exserted well beyond bracts, sharply to somewhat obscurely trigonous, narrowly oblong, the sides remaining ± parallel to the deeply 3-lobed mouth, the lobes free for ca. 0.25–0.35 the perianth length; lobes deeply bifid, the segments subcaudate to caudate, entire or sparingly dentate-ciliate-laciniate, the lobes with a few accessory teeth, cilia or laciniae below the level of the segments; keelar wings common, of several cells high, armed with a few teeth or cilia.

Seta 7 cells in diam., with 21 rows of outer cells surrounding an inner core of scattered cells with corners thickened as in knot-like trigones, the outer ring of core cells ± similar to epidermal cells or feebly smaller, the interior core cells larger than epidermal cells. Capsule broad elliptic, 735 × 560 µm to 875 × 735 µm, the wall 43–52 µm thick, of 5–6 (locally 7) layers, the outer layer of cells equal to thickness of 2.9–3 of interior strata; outer layer of cells subquadrate to short rectangular even at valve base, the radial walls thin, with red-brown nodular to feebly spine-like thickenings, the thickenings mostly on longitudinal walls, sporadically on transverse walls, the cells often with one of longitudinal walls with more thickenings than opposing longitudinal wall of same cell (which may be free of thickenings), but the capsule wall without consistent tendency toward two-phase development, the outer layer only rarely with semiannular bands and then near end of cell; intermediate layers subequal to one another, but each somewhat thicker than inner layer, the intermediate layers with vertical thickenings often feebly tangentially extended; inner layer of cells irregularly long rectangular, the vertical walls with local development of sheets of red-brown wall material, with semiannular bands red brown, common, often incomplete, the radial walls with nodular to spine-like thickenings often present on both longitudinal and transverse walls.

Spores 13–14.4 µm, pale brown, with dense, low but sharply defined, close papillae and short-vermiculate markings; spore:elater diameter ratio 1.8–2:1. Elaters tortuous, 6.2–7.7 µm wide, the spirals 2.4 µm wide.

DIFFERENTIATION—*Chiloscyphus bisipinosus* should offer no confusion either in the field or in the laboratory. The habitat and growth pattern are distinctive—typically it is terrestrial and prostrate to erect, commonly in notably loose mats; it rarely occurs in thick, pure dense mats, and if at all tufted, then the tufts are small and noncompact. The light green or pale yellow green translucent leaves also are distinctive. The leaves are deeply divided (mostly 0.4–0.55) by acuminate to subcaudate lobes that terminate in a uniseriate row of 4–11 cells (Figs. 10: 12; 13: 7). The basal portion of the lobes and at least the distal portion of the lamina are bordered by 1 (sometimes locally 2) rows of enlarged cells, which may be easily distinguished under the dissecting microscope (Figs. 10: 12; 13: 7; see under Notes). The dorsal and ventral margins of the leaf are entire or 1–2-ciliate; the ventral margin, especially in larger phases, is sharply and abruptly reflexed in the basal half (Fig. 10: 1). The underleaves are divided nearly to the base, and the long acuminate to subcaudate, ventrally sulcate lobes also have a border of large cells (Fig. 10: 2). The underleaves have a pair of lateral processes that are variable in stature, and when large, the underleaves are 4-lobed (Fig. 10: 1, 9, 10).

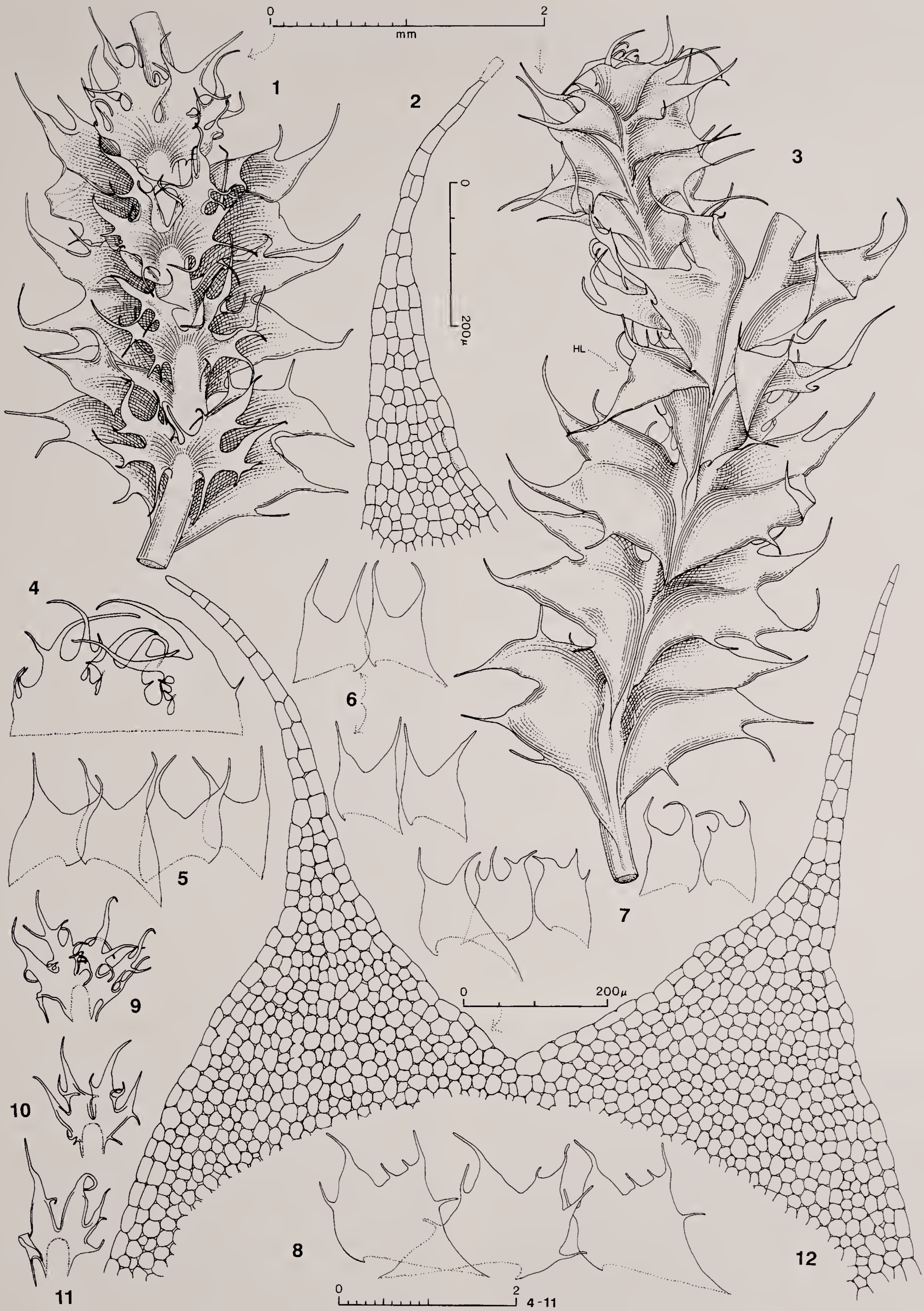


FIG. 10. *Chiloscyphus bispinosus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. (Robust phase). **1.** Sector of main shoot, ventral view. **2.** Distal portion of median lobe of underleaf. **3.** Portion of shoot with *Frullania*-type branch, dorsal view; note unlobed half-leaf (= HL). **4.** Perianth mouth, ventral lobe in middle. **5–8.** Leaves, each from a single shoot; note intra- and interpopulation variability. **9–11.** Underleaves. **12.** Distal portion of leaf. (**1, 3, 8, 9,** from *Schuster 67-584*, New Zealand, North Is., Ruahine Mtns.; **2, 10–12,** from *Engel 18402*, New Zealand, South Is., Arthur's Pass Natl. Park; **4,** from *Engel 18416*, New Zealand, South Is., Arthur's Pass Natl. Park; **5,** from *Engel 18983*, New Zealand, South Is., track to Alex Knob; **6,** from *Child 2914*; New Zealand, South Is., Siberia Hut; **7,** from *Child 3833*, South Is., Lammermoor Range.)

Larger phases of this species initially may be confused with *Chiloscyphus cuspidatus*, in that both are similar in stature and have distinctly bilobed, ovate-trapezoid leaves that have piliform lobe tips and that may have teeth on the ventral margin. The two species also share such features as free, deeply divided underleaves with a reduced lamina, and subcaudate-caudate underleaf lobes with often opposing armature. Care is especially needed because *C. bispinosus*, which is confined to New Zealand, and *C. cuspidatus* are not ecologically differentiated; the two species often occur at the same site and may be intermixed (e.g., *Engel 18201*). *Chiloscyphus bispinosus*, however, is immediately separable by the presence of a border of larger cells on leaf and underleaf lobes, the smaller cell size, the often sulcate leaf lobes, and the dioecious condition. After some experience with this complex, the student will be able to recognize this cell size differential under the dissecting microscope. Also, *C. bispinosus* often develops larger trigones, which are nearly always distinct. Populations having leaves with small, concave-sided trigones are usually accompanied on the same shoot by medium, straight-sided trigones. Populations with trigones ranging from medium to large and ± knot-like are common. Uniformly minute as well as uniformly distinctly knot-like trigones are exceptional. *Chiloscyphus cuspidatus* has uniformly minute to small trigones.

Larger phases of *C. bispinosus* also may be confused with the allied *C. subporosus*. See the Differentiation section under that species for discussion.

The sharply deflexed ventral margin of the leaf is a valuable taxonomic character but must be considered in combination with other diagnostic features of the species, such as free underleaves, piliferous leaf tips, small cell size, etc. Unrelated species in both *Chiloscyphus* and *Heteroscyphus* also have deflexed ventral margins, and it seems that this character was given undue emphasis and served as the basis for numerous misidentifications.

VARIATION—For a considerable period of time I had recognized a robust phase of *C. bispinosus* as a distinct species; I had no name for that species. I took this position because my early concepts of the complex were based on a limited suite of specimens that fit into opposing ends of a broad spectrum, without intermediates at hand. It is useful to be aware of and to understand these extremes, and a key is therefore provided.

Key to Extreme Phenotypes of *C. bispinosus*

1. Plants very small and threadlike, to 1.8 mm wide, the tips often attenuated and with small leaves; leaves distant to contiguous, 220–650 μm wide, basically symmetric or nearly so, oblong-ovate to oblong rectangular to cuneate, 1.3–2.5× longer than wide, the lamina mostly widest in median or distal third, the dorsal margin not decurrent; underleaves 1.3–1.6× stem width, the median lobes 3–9 cells wide at base, the lobe margins entire; half-leaf of terminal branches subcaudate to piliform; oil-bodies 2 per cell . . . . diminutive phase

1. Plants large, to 2–3.2 mm wide, the tips not attenuated; leaves loosely imbricate, 800–2000 μm wide, asymmetric, short- and wide-subrectangular to wide ovate to trapezoid, 0.75–1.2(1.4)× longer than wide, the lamina uniformly widest near the base, the dorsal margin long decurrent; underleaves (1.5)2–2.8× stem width, the median lobes (10)13–20 cells wide at base, the lobe margins with a few cilia or laciniae; half-leaf of terminal branches narrowly acute; oil-bodies 2–3(4) per cell . . . . robust phase

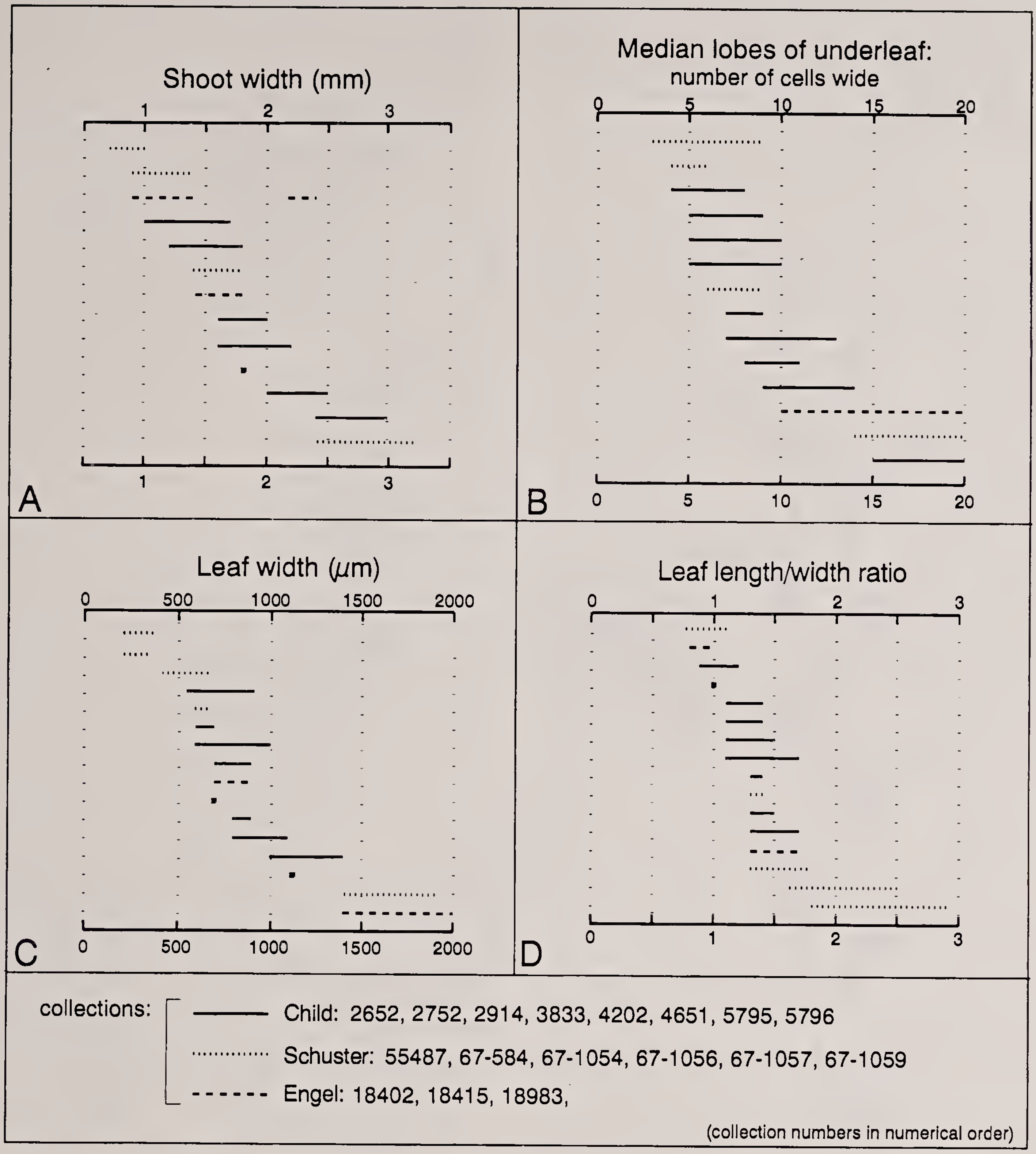
Representative specimens of the small phase are *Schuster 67-1054a*, *67-1056a*, and *55487*, whereas those of the large phase are *Engel 18402*, *Schuster 67-584*, and *Child 4651*. The graphs in Tab. 4 illustrate not only the spectrum of variability of several of the main characters in the key above, but that the extremes are quite distinct, with no character overlap. However, because larger numbers of specimens of the complex were examined, a continuum involving each of the distinguishing characters became evident (Table 4). Some of these intermediate collections were selected and measurements of their character states placed in each of the graphs.

In general, increase in plant size is accompanied by a gradual shift in leaf shape. Small shoots have basically oblong-ovate to oblong rectangular, ± symmetric leaves that are always longer than wide and nearly always widest in the median or distal third of the leaf, frequently with both dorsal and ventral margins curved and narrowed toward the base (Fig. 13: 4, 5). With increase in shoot vigor, leaves tend to be dilated in the basal sector, where the leaves of such plants are widest, lending a wide ovate to trapezoid shape, commonly with the ventral margin sharply curved near the base and the dorsal margin straight or curved inward (Fig. 11: 2, 8). This shape change is accompanied by a shift in symmetry to sharply asymmetric leaves. Intermediate populations often have a mixture of leaves (on one shoot), some being longer than wide, others wider than long. Because a continuum is involved with this intriguing variation, I cannot recognize infraspecific categories.

Branch type is variable, even at the same site. For example, *Engel 18402* from Kelly Range has nearly exclusively *Frullania*-type branching, with only a single lateral-intercalary branch observed. *Engel 18415* from the same locality, however, has *Frullania* and lateral-intercalary types both common, with the latter slightly more predominant. Ventral-intercalary branches also are present, although sporadic, in the latter. *Engel 18777*, from a different locality, also had overwhelmingly terminal branches—of the 65 sterile branches seen, only five were lateral-intercalary. In that collection androecia were exclusively on *Frullania*-type branches (50 seen).

A small (shoots 450–630 μm wide), wire-like phase with dorsally assurgent leaves should be treated with great care because of possible confusion with *Clasmatocolea inflexispina*. That species and *Chiloscyphus bispinosus* share such features as large trigones, presence of a leaf border of large cells, and deeply divided leaves (0.4–0.55-fid). Potential confusion especially occurs on those shoots of this phase possessing concave leaves with nonattenuated to at most feebly piliform lobes. Under these circumstances several shoots must be surveyed to check expression of characters diagnostic for either species. *Child H 3175* (which has young gynoecia) serves as an example of this phase. Median leaf cells are 20–26 μm wide × 23–30 μm long, and thus considerably larger than those of *Clasmatocolea inflexispina* (which has isodiametric cells 10–14 to up to 17–23 μm wide and long) but within the range of *Chiloscyphus bispinosus*. The Child specimen has sporadic leaves with a tooth on the ventral margin;

TABLE 4. Comparison of populations of *Chiloscyphus bispinosus*.



Clasmatocolea inflexispina has uniformly entire leaves. Whereas underleaves of the Child specimen have variability of sinus depth (which is not unusual for a population bearing young gynoecia), sterile shoots have underleaves deeply divided, with a depth beyond the range of *C. inflexispina* (which is 0.65–0.75-fid). Leaf lobe tips are a valuable diagnostic tool for *C. inflexispina*; they nearly always terminate in one cell or a uniseriate row of at most 2 cells (see Engel, 1990b). Lobe tips of the Child specimen have a uniseriate row of (2)4–6(8) cells; thus, it is within the range of *Chiloscyphus bispinosus* but beyond that of *Clasmatocolea inflexispina*.

It appears that this phase is an ecotype and that these characters are expressed when plants occur erect in rather dense tufts. As above mentioned, the species normally does not form tufts.

A rare phenotype characterized by large stature and polymorphous leaf apices should be treated with care to separate the population from *C. villosus* (*Child 2519* is an example). In such cases, one must make a careful search for leaf surface ornamentation (for notes on variability of expression of surface ornamentation, see p. 191).

NOTES—1) Leaf border: The leaf border is normally well defined and easily observable under the dissecting microscope. The border is optimally differentiated by the 1–2 rows of distinctly larger cells at the margins of the lobes, the sinus base and the distal half of the lamina (Fig. 10: 12). However, at times, the border is ill-defined, as in *Schuster 60176*. In such cases careful search is required using a number of different shoots, especially larger ones that usually occur intermixed. In such cases, leaf dissections should be made because flattened preparations better reveal the suboptimal or feeble expression of the character. Sometimes only the ventral margin has a differentiated border; other leaves have both dorsal and ventral margins bordered, but lack a border at the lobes and sinus base.

Rare populations totally lack differentiation of a leaf border, and in such cases one must rely on the combination of free underleaves that are divided nearly to the base,

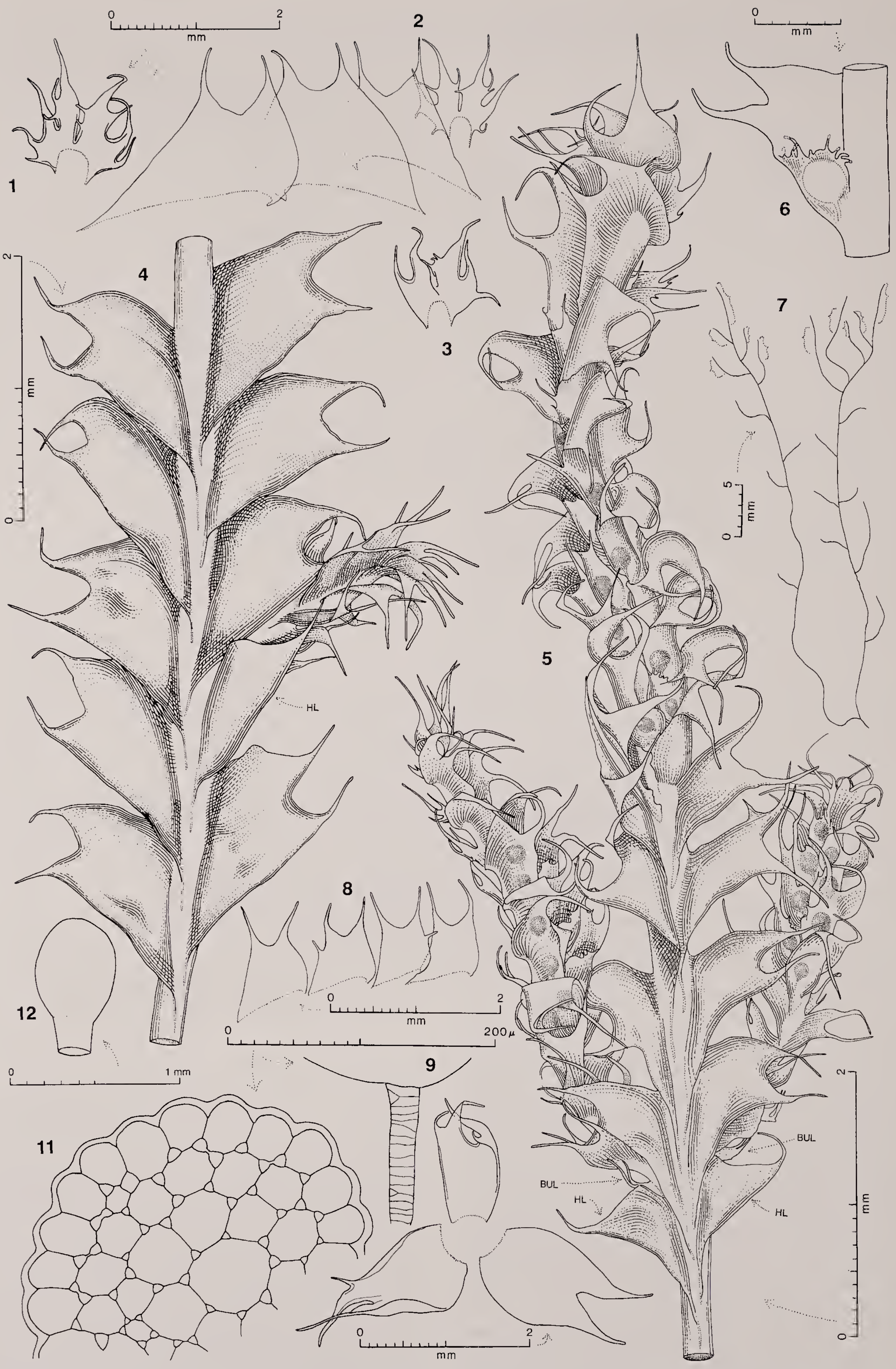


FIG. 11. *Chiloscyphus bispinosus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. (Robust phase). **1–3.** Leaf and underleaf outlines. **4.** Portion of shoot with *Frullania*-type branch, dorsal view; note unlobed half-leaf (= HL). **5.** Plant with androecia on main shoot and 2 *Frullania*-type branches (HL = half-leaf; BUL = 1st branch underleaf). **6.** ♂ Bract, *in situ*. **7.** Cladograph, all branches of *Frullania* type, brackets indicate area of androecia. **8.** Leaves. **9.** Antheridial stalk. **10.** ♀ Bracts and middle upper, bracteole. **11.** Seta, cross section. **12.** Capsule profile. (**1–4,** from *Engel 18402*, New Zealand, South Is., Arthur's Pass Natl. Park; **5–7, 9,** from *Engel 18777*, New Zealand, South Is., Fiordland Natl. Park; **8,** from *Child 5796*, New Zealand, South Is., Rock and Pillar Range; **10,** from *Engel 18416*, New Zealand, South Is., Arthur's Pass Natl. Park; **11, 12,** from *Allison H3381*, New Zealand, North Is., near Atiamuri.)

piliferous leaf lobes, and cell size to distinguish it from allies. Time invested in search of the border character is essential because no other member of the section develops such a border (except sometimes *C. subporosus*), and the character is expressed, at least feebly, in the vast majority of populations.

2) Gynoecial shoots of smaller phases of the species often appear quite different from sterile shoots (e.g., *Schuster 67-1057a*). The different appearance results from leaves occasionally being less deeply bifid (sometimes only to 0.3) and the less deeply divided underleaves. Because deeply divided leaves and underleaves are important diagnostic features for the species, such shoots must be treated very carefully. To confirm whether or not gynoecial plants are at hand, particularly when ♀ plants are young, one must check for the presence of archegonia. Gynoecial shoots often prevail, with sterile shoots difficult to find.

Gynoecial shoots (even ♀ in early phases) often are larger than sterile ones. Sterile compared with gynoecial shoot size differences are often distinct, such that populations often superficially appear to be an admix of two taxa differentiated by size. Sterile and gynoecial subfloral innovations originating from the same parent shoot serve to illustrate the interesting contrast and definitively confirm that one genotype may exhibit a rather broad spectrum of variation (e.g., *Engel 18959*). Care must be taken to identify sterile shoots for study; other than the sterile shoot characters noted immediately above, the leaves are of uniform size throughout, and are ± equidistant. Leaves of female plants increase in magnitude and become more closely imbricate toward the gynoecium; this is accompanied by progressively shallower underleaf sinuses.

3) Lateral armature of the underleaves is variable in stature and position. A process grading in magnitude from tooth to lacinium is positioned on the disc, or if toward the base of the main lobe, then obviously above the level of the main underleaf sinus and therefore part of the lobe and not disc. If the lateral process was positioned on the lobe, then the number of cells across the lobe base was measured at a point immediately distal to the process. Measurements are more reliable at this locus because underleaves are often dilated at the base of lateral armature.

NOTES ON TYPE SPECIMENS—1) *Jungermannia bispinosa* Hook. f. & Taylor. The uniformly entire leaves are strongly dorsally assurgent, suberect (Fig. 12: 3) and (typical of the diminutive phase) distant to contiguous (Fig. 12: 1–3). The leaf border of larger cells is only feebly developed on some shoots and moderately so on others. Trigones are large and bulging to weakly knot-like (Fig. 12: 7). I saw no trace of sex organs. The plants agree with the diminutive phase (as defined in the Key to Extreme Phenotypes of *C. bispinosus*, p. 34), except the dorsal margin is moderately decurrent.

Four specimens from Campbell Is. are at BM: two collected by Hooker, two without collector. All of these specimens, together with Hooker-collected plants at FH and S, appear to be part of the same collection, which contains somewhat flaccid plants.

2) *Lophocolea mittenii* Steph. The plants represent the diminutive phase of *C. bispinosus*. Leaves are ca. 0.45–0.55-fid, entire margined, with ventrally sulcate lobes and a well-developed border of enlarged cells. Trigones are medium to large and with sides straight to slightly bulging. Underleaves have margins reflexed and lobes ventrally sulcate. Gynoecia in the pre–leaf fusion stage are present.

3) *Lophocolea minuta* Pearson. The plants are a small extreme of the diminutive phase, and Pearson (1923, p. 377) remarked, "*Lophocolea minuta* is one of the smallest perfectly developed species of the genus I have seen." The plants are rather flaccid and have entire-margined leaves with a rather well-defined border of enlarged cells. Underleaves are large for the shoot size. The protologue states that androecia are present, but I have not seen them.

4) *Lophocolea curvifolia* Herzog. Label information does not match protologue data for all original specimens. The protologue bears the following locality and collector: "Marlborough, leg. J. H. McMahon, 1929." I have seen two specimens of this name: one from CHR, the other from JE. The CHR specimen has label information that matches the protologue and also notes "Mrs. E. A. Hodgson No. 6 to Herzog. Type of *Loph. curvifolia* Herzog." The JE specimen disagrees with the protologue in having Wairoa, New Zealand, as locality and E. A. H(odgson) as collector, but agrees with it in having number 6 and the year 1929. I have no explanation for this discrepancy. Because both collections contain indistinguishable plants, including a few admixed plants of *Riccardia* sp. and *Fissidens* sp., I conclude that they indeed are segregates of the same specimen and that the JE label is in error.

A second packet mounted on the same sheet as the above-mentioned specimen from JE bears a packet with a label bearing "TYPUS. aus Glyzerin-Präparat der Herzog-Samml. herbarisiert durch Grolle 1981. no. '6'." The packet contains several shoots, one of which has the only perianth seen. The perianth is immature, which accounts for the "anguste campanulata" shape given to it by Herzog.

The plants represent the diminutive phase of the species. The leaves have a well-developed border.

DISTRIBUTION—Amphipacific: Macquarie Is.; Campbell Is.; New Zealand (Stewart Is., South Is., North Is.); Falkland Is. (Engel, 1990a); Isles of Scilly (Paton, 1974); and Isle of Colonsay, Scotland (Wallace, 1979). Specimens labeled *L. bispinosa* from Tasmania are misdeterminations of *C. subporosus*. Reports from Australia require confirmation. Reported from southern South America by Massalongo (1885, 1927); these, however, are misdeterminations (Engel, 1990a).

ECOLOGY—In New Zealand, *C. bispinosus* occurs over a broad altitudinal gradient: 50–1585 m on South Is. and 305–1370 m on North Is.

In forests, the species usually is associated with wood and particularly very rotted, decorticated logs that have accumulated some soil and a bryophyte cover. It also occurs on bark of dead trees and on bark chunks on the forest floor. It may be terricolous on shaded, damp banks or hillsides (under cover of, e.g., manuka, bracken or grass) or in boggy sites.

In the subalpine-alpine zone it often occurs terricolous as loosely creeping tufts in damp situations, such as under snow tussock or scrub or on banks, steep slopes or boggy ground in seepage areas. In these niches, the species may form pure carpets that may extend onto the bases of vascular plants. It also occurs over soil on banks of small watercourses, on soil over rock in protected niches (e.g., crevices) or in shady scrub, or at times on boulders in exposed sites.

On Campbell Is. the species occurs in herbfields with grasses, sedges, and mosses (it may be intermixed with *Breutelia*, e.g.).

The species appears to be ecologically rather aggressive, in that it may occur, for example, on moist planking at the margin of a concrete dam.

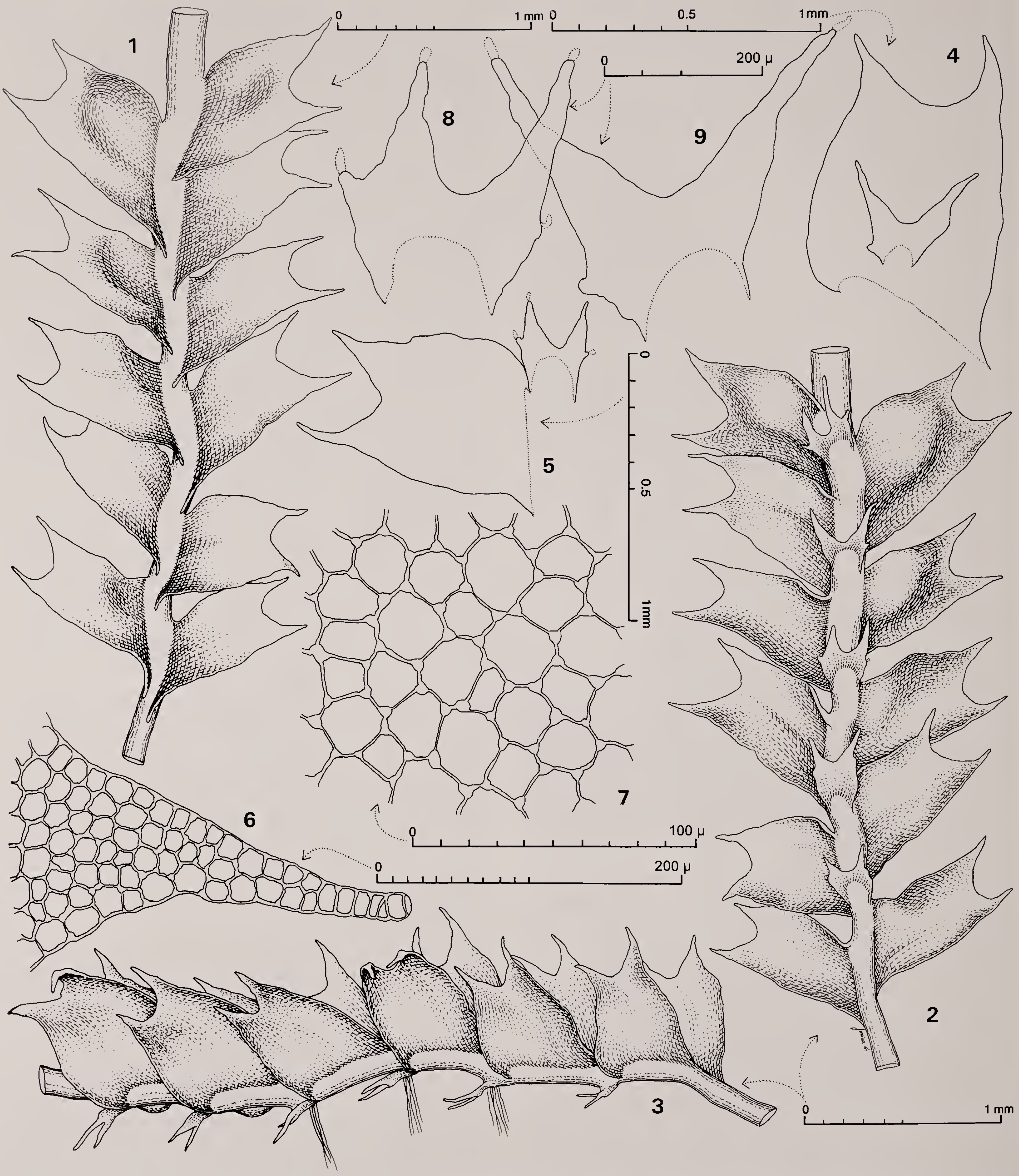


FIG. 12. *Chiloscyphus bispinosus* (Hook. f. Tayl.) J. J. Engel & R. M. Schust. **1.** Main shoot, dorsal view. **2.** Main shoot, ventral view. **3.** Main shoot, lateral view. **4.** Leaf and within, underleaf. **5.** Leaf and adjacent underleaf. **6.** Leaf segment. **7.** Median leaf cells. **8, 9.** Underleaves. (All from type of *Jungermannia bispinosa* [FH].)

Chiloscyphus bispinosus has a characteristic appearance in the field. The plants are pale yellow green to a very pale, and often bright light-green, and typically grow very loosely creeping to ascending to erect, at times tending to form small tufts. Plants often have a loosely sprawling, noncrowded habit and grow almost weft-like over the substrate. The species only exceptionally forms thick, pure, dense carpets. Good field characters are the deeply bilobed leaves with caudate lobes and the convex lamina.

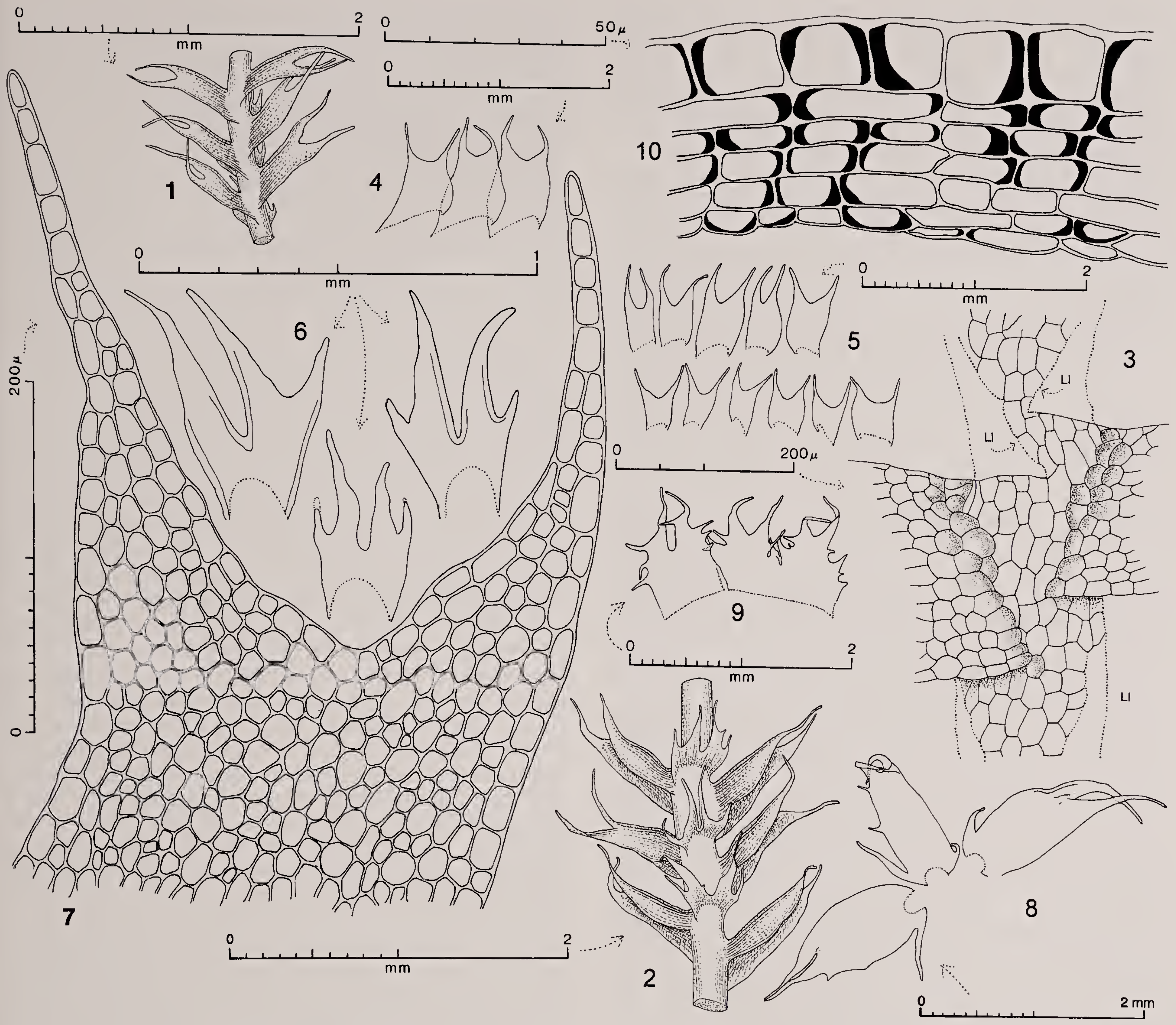


FIG. 13. *Chiloscyphus bispinosus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. (Small phase). **1.** Sector of main shoot, dorsal view. **2.** Sector of main shoot, ventral view. **3.** Portion of stem to show leaf insertion lines (li = line of insertion); dorsal view. **4.** Leaves. **5.** Leaves, note variation in symmetry. **6.** Three underleaves. **7.** Distal half of leaf. **8.** ♀ Bracts, and in middle, bracteole. **9.** Perianth mouth, ventral lobe in middle. **10.** Capsule wall, cross section. (**1, 2, 5 (top row), 6,** from *Schuster 67-1054a*, New Zealand, North Is., North Auckland Prov., Mangamuka Gorge Reserve, N of crest, ca. 305 m; **3, 5 (bottom row), 7–9,** from *Schuster 67-1056a*, same loc.; **4,** from *Schuster 67-1057a*, same loc.; **10,** from *Engel 17839*, New Zealand, South Is., Westland Prov., Mt. Aspiring Natl. Park, off track to Mt. Brewster, below and W of Mt. Armstrong.)

SPECIMENS SEEN (selected)—**CAMPBELL IS.:** without specific loc., *1958 Expedition s.n.* (CHR); ibid., *1960 Expedition s.n.* as *L. bidentata* (CHR); Mt. Beeman, ca. 75 m, *1958 Expedition s.n.* as *L. bidentata* (CHR); ibid., *Rae s.n.* as *L. bidentata* (CHR); near top of Mt. Juma, ca. 470 m, *Taylor s.n.* (AKU); summit of Mt. Honey, 600 m, *Meurk H8311* (WELT); Buchanan Valley, 150 m, *Meurk H8290*, *H8293* (WELT). **AUCKLAND IS.:** Stony Peak, 480 m, *Johnson 1515* (WELT). **NEW ZEALAND. STEWART IS.:** Halfmoon Bay (Oban), Horseshoe Bay Road, ca. 10–30 m, *Engel, von Konrat & Braggins 24682* (F); Port Pegasus, *Schuster et al. s.n.* as *L. bidentata* (CHR). **SOUTH ISLAND. SOUTHLAND:** Lake Hauroko, ca. 120 m, *Child 1588* (F); Garvie Range, East Dome, ca. 1385 m, *Child H 3904* (F); Fiordland Natl. Park, head of Lake Manapouri to Wilmot Pass, *Simpson s.n.* (CHR); ibid., Cascade Creek, near Lake Gunn, Eglinton Valley, *Schuster 55487a* (F); ibid., Central Earl Mtns., Mistake Creek, between Triangle Peak and Melita Peak, NE of N end of Lake Te Anau, 740–800 m, *Engel 18777* (F); ibid., Milford Track, Sutherland Falls, *Morice et al. s.n.* (CHR); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18824* (F). **OTAGO:** Catlins River area, Ajax Swamp, ca. 1 km N of Ajax Hill, ca. 455 m, *Child H 5483*, *H 5524* (F); Glenledi, ca. 120 m, *Simpson s.n.* (CHR); Akatore, *Allison H 1353* (CHR); Akatore Stream, *Allison H 1361* (CHR); near Clarendon, S of Dunedin, ca. 60 m, *Allison H 5384* (CHR); near Berwick, ca. 245 m, *Allison H 1350* (CHR); Maungatua, E face, W of Mosgiel, ca. 610 m, *Child H 1519*–c. sporo. (F); Dunedin, Swampy Hill, ca. 610 m, *Child H 2652* as *L. inflexifolia* (F); Leith Valley, ca. 305 m, *Allison H 3720* (CHR); ibid., Morrison's Creek, outskirts of Dunedin, ca. 90 m, *Fife 6732* as *L. novaezeelandia* (F); ibid., ibid., *Simpson s.n.* (CHR); Lee Stream, ca. 305 m, *Child H 2519* as *L. inflexifolia* (F); near Lee Stream, Hindon Road, ca. 305 m, *Child 900* (F); Mt. Cargill, N of Dunedin, ca. 455 m, *Child H 771* as *L. lenta*–c. ♂, *H 791* (F); Silverpeaks, N of Dunedin, ca. 670 m, *Child H 5589* (F); Lammermoor Range, ca. 610–760 m, *Child H 3480* (F); Rock and Pillar, ca. 1065–1310 m, *Child 2752*–c. per. (F); ibid., S end, WNW of Middlemarch, near McPhees Rock, ca. 1220 m, *Child H 3862* as *L. novaezeelandiae*, *H 5796* (F); near Herbert, S of Oamaru, *Allison H 1386* (CHR); Serpentine Diggings Road, ca. 915 m, *Child H s.n.163* (F); Trotters Gorge, ca. 60 m, *Child H 4415* (F); Old Man Range, ca. 1 km N of summit of Shingle Creek Road, SW of Alexandra, ca. 1370 m, *Child H 3892* (F); near Naseby, 610–700 m, *Allison H 5444* as *L. decurrens* (CHR); Hawkdun Range, ca. 915–1585, *Child 508* as *L. bidentata*, *H 3175* as *L. amplectens* (F); W Matukituki Valley, headwaters, ca. 1160 m, *Child H s.n.168* as *L. inflexifolia* (F); Dunstan Range, ca. 1525 m, *Child 1673* as *L. inflexifolia* (F); Fiordland Natl. Park, Humboldt Mtns., N side of Earland Falls, on track to Lake Mackenzie, *Schuster 67-3454B* (F); ibid., head of Lake McKerrow, *Hatcher 979* (F); opposite Siberia Hut, WNW of Makarora, ca. 1065, *Child 2914* (F); Haast Pass Road, near Fish River, just S of Haast Pass, ca. 455 m, *Child H 1918* (F); near top of Haast Pass, ca. 565 m, *Allison H 5974* (CHR). **WESTLAND:** Mt. Aspiring Natl. Park, 0.7 km N of Haast Pass and just S of Cross Creek, 525 m, *Engel 23089* (F); ibid., off track to Mt. Brewster, below and W of Mt. Armstrong, SW of Mt. Brewster, ca. 900 m, *Engel 17839*–c. sporo. + ♂ (F); ibid., Mt. Brewster, ca. 1370 m, *Child H 4202* as *L. inflexifolia* (F); Lake Moeraki, *Braggins 75/209* (AK); Copland Valley, ca. 1220 m, *Child H 4651* (F); near township of Fox Glacier, ca. 0.5–0.6 mi. from front of Fox Glacier, *Schuster 60176* (F); near Fox Glacier, *Mues NZ 48a* as *L. lenta* (F); Westland Natl. Park, track to Alex Knob, off track to Louisa Peak, 1170 m, *Engel 18983*–c. ♂ + per. (F); NW of town of Franz Josef Glacier, off Hwy 6, near Waiho River between Lake Wombat Terrace and Canavans Knob, 110 m, *Engel 18959*–c. ♂ (F); Arthur's Pass Natl. Park, Kelly Range, off track to Carroll Hut, above Kellys Creek, N of Otira, 1040–1110 m, *Engel 18402*–c. ♂, *18421*–c. sporo. (F); Camp Creek, W of Alexander Range, 630–800 m, *Reif C223C* as *C. lentus*, *C264A* as *C. inflexifolius* (F). **WESTLAND/CANTERBURY BOUNDARY:** Arthur's Pass Natl. Park, Otira Valley Track, along Otira River, NE of Mt. Rolleston, 1210–1310 m, *Engel 22910* (F); ibid., Arthur's Pass, near Temple Basin Ski Area, *Engel 6474* (F). **CANTERBURY:** Banks Peninsula, Reynolds Valley Road, ca. 1 km below junction with Bossu Road, ca. 190 m, *Fife 6833* (F); Mt. Cook Natl. Park, Tasman Valley, Birch Hill marshes, ca. 670 m, *Wilson 2504* (CHR); ibid., Governors Bush, SW of town of Mt. Cook, 760–800 m, *Engel 18200*–c. ♂, *18201* (F). **NELSON:** Near mouth of Sphinx Cave, ca. 1060 m, *Brown s.n.* as *L. bidentata* (AK); Kahurangi Natl. Park, Garibaldi Ridge, vicinity of Gordon's Pyramid, 1335 m, *Engel & von Konrat 27103*. **MARLBOROUGH:** Without specific loc., *McMahon s.n.* as *L. inflexifolia* (CHR). **NORTH ISLAND. WELLINGTON:** Gollans Valley, *Moore s.n.* as *L. mitteniana* (CHR); Wellington, Hawkins Hill, *Moss s.n.* (AK); Wairongomai River, *Zotov s.n.* (CHR); Tararua Range, Akatarawa Forest Park, *Mues NZ 47a* (F); Hemimatenga Scenic Reserve near Waikanae, *Mues NZ 47* (F); W Ruahine Mtns., Whanahuia Range, 1–1.5 mi. Wof Mt. Mangahuia, ca. 1370 m, *Schuster 67-584* (F); Tongariro Natl. Park, Ruapehu, ca. 1160 m, *Selling s.n.* (S); ibid., Mt. Ruapehu, Silica Spring Track, *Braggins s.n.* (AK). **HAWKES BAY:** Puketitiri, *Hodgson 301*, *302*–c. per. (CHR); Wairoa, *Hodgson 621* as *L. graminicola*, nom. herb. (CHR), *s.n.* as *L. graminicola*, nom. herb. (F); ibid., "Kiwi," *Hodgson 53*, *136* (CHR); ibid., Te Tiki, *Hodgson 622* as *L. glomerata*, nom. herb. (CHR). **GISBORNE:** Waikaremoana, *Butler 2183* (CHR). **SOUTH AUCKLAND:** E of Taupo, ca. 610 m, *Allison H 3528* (CHR); near Atiamuri, S of Rotorua, ca. 305 m, *Allison H 3381*–c. sporo., *H 3396*, *H 3478*, *H 3479*, *H 3527* (CHR); Okere Falls, NE of Lake Rotorua, *Schuster 67-4380B* (F); Urewera Natl. Park, track from NS road to Mt. Whakataka, 945–1100 m, *Schuster 67-1603* (F); E of Waiotapu Valley, 490–550 m, *Allison H 3418*, *H 3426* (CHR); Tarawera, ca. 610 m, *O'Malley s.n.* (CHR); Mt. Tarawera, Bay of Plenty, *Braggins 84/329B* (AK); Coromandel Peninsula, *Matthews 124pp* (CHR). **NORTH AUCKLAND:** Mangamuka Gorge Reserve, N of crest, SE of Kaitaia, NW of Mangamuka, ca. 305 m, *Schuster 67-1054a*, *67-1056a*–c. per., *67-1057a* (F). **LITTLE BARRIER IS.:** Parihakoakoa Stream, *Braggins 84/287* (AK).

Chiloscyphus subporosus (Mitt.) J. J. Engel & R. M. Schust.

Lophocolea subporosa Mitt. *in* Hooker, Bot. Antarc. Voy. 2: 137. *pl. 97, f. 3.* 1854. *Chiloscyphus subporosus* (Mitt.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 423. 1985 (1984). Type: New Zealand, North Is., Auckland, *Sinclair* (BM!–c. per., FH = *absens*, G = *absens*, NY = *absens*); *ibid.*, North Is., Wellington, *Stephenson* (BM = *absens*, FH [hb. Steph.]!, G!, NY = *absens*).

Plants often rather fragile, ascending to erect but prostrate at extremities of population where over bare substrate, pale green to greenish yellow, translucent; shoots to 3 mm wide. Branches common, some populations with exclusively *Frullania*-type vegetative branching (the half-leaf undivided, or if bifid, then of similar form to vegetative leaves), lateral-intercalary branching rare. Stems 11–12 cells high, the cortex poorly differentiated laterally and dorsally, in 1 row of feebly smaller cells, the ventral cortical cells moderately well differentiated, in 2 (locally 3) rows of cells somewhat smaller than those of medulla; cortical and medullary cells thin walled. Rhizoids in tight fascicles from stem at immediate base of underleaf. Leaves often translucent, alternate, dorsally assurgent at least in basal sector and sometimes strongly so throughout, widely spreading, loosely imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end or weakly so and then comma-like, the long decurrent strips of dorsal margin often parallel, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells (the insertion of opposing leaves often extending to laterally juxtaposed rows of stem cells and not to exact midpoint of stem). Leaves gradually and gently convex but feebly so on leaves that are strongly dorsally assurgent, asymmetrically ovate-trapezoid to ± ovate (often markedly broadly so), at times subsymmetric (when leaves are broad ovate and on suboptimal shoots), conspicuously widest near base; apex bifid to 0.15–0.3 (polymorphous and 1-lobed to retuse in sporadic suboptimal phases), the lobes ± parallel to slightly diverging, plane, the ventral often conspicuously larger, the lobes variable: ranging from (occasionally) medium to broad acute to apiculate to acuminate to subcaudate, terminating in a uniseriate row of 2–8(11) cells that are wider than long, isodiametric, or at most moderately longer than wide, being 11–20 µm wide × 17–31 µm long or 1.1–2.1× longer than wide, the lobe margins entire, the sinus rounded, often lunate, rarely and sporadically with a tooth; dorsal margin feebly curved outward but more often ± straight to curved inward and lunate, plane to slightly deflexed, entire; ventral margin broadly and conspicuously arched, plane (if reflexed [rare] then only in robust extremes), entire, rare and sporadic leaves with 1 spine. Lobes and at least the distal portion of lamina often bordered by a row of enlarged cells that are often crenulate, the border at times feeble or lacking. Leaf cells dimorphic: most small, but scattered throughout leaf (often in clusters or rows) are conspicuously enlarged intramarginal cells lending the leaf a speckled appearance; nonenlarged median leaf cells 18–32 µm wide and long, the enlarged cells in median and apical sectors of leaf 29–40(44) µm wide × 30–44 µm long; walls notably thin, trigones minute to small or lacking; surface smooth. Oil-bodies throughout leaf, colorless, in leaf middle 2–4 to 4–8 to 5–10 per cell, coarsely granular to finely botryoidal, elliptic to fusiform, less often crescentic, a few subglobose and 3.9–4.6 µm in diam., 6.5–7.8 × 3.3–3.9 µm to 8.5–10.4 × 3.3–4.6 µm. Underleaves polymorphic, much smaller than leaves, 1.7–2.6× stem width, free on side nearest to adjacent ventral base of leaf, long decurrent and free or obscurely connate on the other, the insertion often asymmetric, inverted U-shaped, the underleaves parallel with stem or slightly spreading, approximate to contiguous, plane, ovate-subrectangular to ± obtrapezoid, the apex bifid to 0.6–0.8(0.85 in suboptimal plants), the lamina variable in height, 5–11(19) cells high on ± optimal shoots but at times only 2–3 cells high on suboptimal ones, the sinus often V-shaped; lobes ± parallel to diverging, narrowly acuminate to caudate, (4)7–13 cells wide at base, terminating in a uniseriate row of (2)3–6 cells (or suboptimally a single cell) that are uniformly slightly to distinctly longer than wide, being 13–22 µm wide × 24–42(48) µm long or 1.1–2.8(4.2)× longer than wide, the lobe margins occasionally feebly reflexed, entire or with 1 or 2 (if the latter, then often opposing) teeth; lamina margins plane (if somewhat reflexed [rare], then only in robust extremes), normally with a single process variable in stature: lobe-like to more often laciniiform to ciliiform, always smaller than main pair of lobes, the lamina margins sporadically with an accessory tooth-like or ciliiform process, conspicuously long decurrent; lobes and at least the distal portion of lamina often crenulate, often bordered by a row of enlarged cells.

Asexual reproduction by regeneration; gemmae lacking.

Plants dioecious, usually sterile. Androecia on leading shoots, or occasionally on elongate, indeterminate, *Frullania*-type branches, or, more often, on lateral-intercalary branches that are either elongate and indeterminate or short, spicate, determinate, and lacking vegetative leaves, the androecia on leading shoots, initially terminal but often eventually become intercalary, the androecia subfolious to spicate, often composed of numerous (up to 22) bract pairs; bracts somewhat to markedly smaller than leaves, the bracts strongly dorsally assurgent (on spicate androecia also erect and vertical), rather tightly appressed to bract immediately above, the saccate portion smooth in profile and fused toward base with opposite bract, the bracts ventricose in basal portion, the distal portion stiffly vertical to distinctly reflexed and more leaf-like in orientation, the apex often similar to leaves in lobe form, at other times (in subspicate or spicate androecia) the lobes becoming reduced and then medium to wide acute to apiculate to even lacking, the apices then retuse to truncate, the ventral margin of bract entire; lobule margin inflexed to involute, the distal sector with a conspicuous tooth-like to acuminate process and basal to process numerous few-celled teeth that terminate in a slime papilla, the sinus between the dorsal margin of the lobe and the distal tooth of the lobule often with 1–2 teeth; antheridia solitary, the stalk long, to 21 cells, uniseriate. Gynoecia on elongate *Frullania*- or lateral-intercalary–type branches of variable length: grading from abbreviated and without vegetative leaves to long; subfloral innovations not seen. Bracts crowded, somewhat *Plagiochila*-like in appearance, transversely oriented, those of innermost series much larger than leaves, erect and ensheathing perianth base, free from one another, narrowly inserted, distinctly convex, narrowly ovate; apex bifid to 0.2, the lobes subequal in size or the ventral somewhat larger, the lobe margins entire; dorsal margin of lamina abruptly deflexed and forming a weak cnemis, usually entire but occasionally with a spinose tooth in distal sector, the ventral margin abruptly deflexed, entire. Bracteoles of innermost series somewhat smaller than bracts, free from bracts, concave (ventral view), narrowly elliptic to obovate; apex bifid to 0.2, the lobe margins entire; lamina margins entire or sparingly denticulate. Perianth longly exserted beyond bracts, sharply trigonous and prismatic throughout, long and narrowly oblong to elliptic, not to slightly narrowing toward the distinctly 3-lobed mouth, the lobes free for ca. 0.25–0.35 the perianth length; lobes distinctly bifid, the segments acuminate, with several often opposing spinose teeth, the lobes otherwise spinose dentate-laciniate in basal sector; keels sharp, with keelar wings common, of a few cells high to conspicuous and then several cells high, often spinose dentate.

Seta 7 cells in diam., with 23–24 rows of outer cells surrounding an inner core of scattered cells with corners thickened as in medium trigones, the outer ring of core cells ± similar to epidermal cells in size or feebly smaller, the interior core cells somewhat larger than epidermal cells. Capsule wide elliptic, the wall 36–38 µm thick, of 4 layers, outer layer of cells equaling or exceeding thickness of all combined interior strata; outer layer of cells subquadrate to short rectangular, the radial walls with magenta nodular thickenings which are on some but not all longitudinal walls and only sporadically on transverse walls, the outer wall with a tendency toward two-phase type of distribution of thickenings (e.g., longitudinal walls with rather dense thickenings alternating with those with few or no thickenings); intermediate and inner layer of cells subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended; innermost layer of cells irregularly short to long rectangular, with semiannular bands red brown, narrow, sometimes incomplete, occasionally forked and then with a few sporadic fenestrae delimited, the radial walls with nodular to spine-like thickenings sometimes present on both longitudinal and transverse walls.

Spores 12.4–13 µm, pale brown, with faint, low but sharply defined, close papillae and short vermiculate markings, spore:elater diameter ratio 1.3–1.6:1. Elaters tortuous, 8.2–10.1 µm wide, the spirals 2.4–2.9 µm wide.

DIFFERENTIATION/VARIATION—The species is highly variable, and portions of two patterns within the variation spectrum are particularly difficult. One pattern grades toward *C. bispinosus* and to a lesser extent *C. cuspidatus*, and the other grades toward *C. lentus*. Each of these patterns is explored below.

Chiloscyphus subporosus* vs. *Chiloscyphus bispinosus—These species form a closely related pair distinguished by the free underleaves, the frequent enlargement of marginal and intramarginal cells (the border of large cells is optimally developed in *C. bispinosus* and dimorphic intramarginal cells in *C. subporosus*), the dioecious condition, and the infrequent production of sex organs. The two species may be intermixed (e.g., *Engel 18402*, *Child H3909*); such collections are valuable for assessment of variation patterns and consistency of characters. *Chiloscyphus subporosus* also has affinities with *C. cuspidatus*, another underleaf-free species. Interrelationships among the three underleaf-free species discussed above are summarized in Table 5.

Chiloscyphus subporosus* vs. *Chiloscyphus lentus—Suboptimal phases of the species require careful treatment because character expression occurs to a lesser, more subtle extent than in optimal, well-developed plants. Plants of *Engel 17704* are valuable in illustrating some of the problems with suboptimal development of the species because some characters are intermediate between well-developed *C. subporosus* and *C. lentus* (Table 6). Furthermore, ecological parameters of the two species overlap, in that *C. lentus* normally occurs on wood and *C. subporosus* commonly so. In Table 6, for example, underleaf disc height of *Engel 17704* may be observed to be closer to *C. lentus* than to ± optimal *C. subporosus*, even though the character is diagnostic on optimal plants. *Engel 18806* also reveals the nature of suboptimal character expression. Some shoots are ± optimal (Figs. 14: 3; 15: 1, 7), whereas others illustrate some of the range of variability of

TABLE 5. Comparison between *Chiloscyphus subporosus*, *C. bispinosus*, and *C. cuspidatus*.

Character	*C. subporosus*	*C. bispinosus*	*C. cuspidatus*
Sexuality	dioecious	dioecious	monoecious
Depth of leaf sinus	0.15–0.3	0.4–0.55	0.2–0.35(0.45)
Leaf border of large cells	often present	present	absent
Dimorphic leaf cells	present	feeble to distinct (esp. in robust phases) or lacking	lacking
Leaf lobe form	plane	often ventrally sulcate	plane
Leaf lobes: no. of cells in uniseriate row	2–8(11)	4–11	5–10(13
Height of underleaf lamina (no. cells high)	5–11 (well-developed plants)	2–4	2–4 (rarely 5–7)
Underleaf lamina margins	plane (reflexed only in robust phases, see text)	reflexed (often distinctly so)	plane to slightly reflexed
Leaf margin armature	usually entire; ventral sporadically with a tooth	dorsal = 1–2 cilia or entire; ventral = 1–3 ciliate-laciniate or entire	entire, sporadically with 1(2) cilia on ventral margin
Trigone size	minute to small or lacking	some small to medium, others medium to large	minute to small
Cell size (median, nonenlarged)	18–32 μm wide and long	13–26 μm wide, 16–30 μm long	28–42 μm wide, 28–54 μm long
Oil-body no.	2–4	2 or 2–3(4)	2–4 to 5–7

C. subporosus, and at the same time some of the pitfalls of certain taxonomic characters when applied to suboptimal shoots. In some shoots, for example, the distal sector consists of leaves and underleaves that appear similar to *C. lentus*, except for the presence of enlarged cells, free underleaves and cells of the uniseriate row of underleaf lobes always being longer than wide. In that shoot sector, the underleaf disc is 2–4 cells high and underleaf lobes 4–6 cells wide at the base, both characters matching those of *C. lentus*. Basal to this is a shoot sector with the diagnostic characters of the species expressed. The underleaf disc is 5 cells high and the lobes 8–13 cells wide at the base. More definitive character expression may be found in *Engel 18812* from the same locality. Here we find the underleaf disc 5–11 cells high, and underleaf lobes 7–13 cells wide at the base and marginal cells somewhat larger and forming an ill-defined to rather distinct border. The underleaf disc also may be bordered by a row of enlarged cells.

Poorly developed populations of the species are particularly difficult to differentiate from suboptimal *C. lentus*. That species and *C. subporosus* differ by presence vs. absence of underleaf connation, a character of important taxonomic value in Lophocoleaceae. Despite the significance of that feature, connation is not reliably expressed in suboptimal populations of *C. lentus*. If underleaf connation is inconspicuous or feeble, see the supplementary key to the *C. subporosus–C. lentus* pair (p. 25). Furthermore, some weak populations of *C. subporosus*, such as *Engel 17714*, *Child 159*, *623*, *2519*, and *2826*, have polymorphic leaf apices, varying from bifid to 1-lobed to retuse to broadly rounded. Sporadic suboptimal populations of *C. subporosus* may have a mixture of free underleaves and those that are very narrowly connate on one side. Such populations may occur on wood, another factor relevant to potential confusion (*Child 304* and *1639* are examples). For these cases, also see the supplementary key to the *C. subporosus–C. lentus* pair (p. 25). Some particularly weak plants are impossible to determine to species level because key characters are irregularly expressed or altogether lacking; such collections are best referred to a "*C. subporosus–C. lentus* complex."

Chiloscyphus subporosus is very closely allied to the widespread *C. latifolius* (Nees) J. J. Engel and R. M. Schust. (= *Lophocolea bidentata* (L.) Dumort.). I have examined several collections of *C. latifolius* from North America and Europe for purposes of comparison. Some populations of *C. latifolius* have dimorphic leaf cells feebly developed, whereas others completely lack scattered enlarged cells. Also, I observed no tendency toward a higher underleaf lamina.

TABLE 6. Comparison between suboptimal and optimal *C. subporosus* and *C. lentus*.

Character	*C. lentus*	*C. subporosus* (suboptimal) (*Engel 17704*)	*C. subporosus* (± optimal)
Leaf symmetry	subsymmetric to symmetric	distinctly asymmetric to subsymmetric	distinctly asymmetric
Leaf lobes: no. of cells in uniseriate row	4–11	(3)4–8	2–7
Leaf decurrence dorsally	at most short	rather long decurrent	conspicuously and markedly long decurrent
Leaf cell trigones	minute to small to (often) medium	minute to small	minute to small or lacking
Height (no. of cells) of underleaf disc	2–4	2–3	5–11(19)
Width of underleaf lobe base (no. of cells)	3–6 (very rarely 7–8)	4–9	7–13
Underleaf lobes: length:width ratio of cells in uniseriate row	wider than long, isodiametric or 1.1–1.6:1	(1.3)1.5–2.8(4.2):1	1.1–2.7:1
Underleaf lobe border	lacking	lacking	ill-defined to distinct

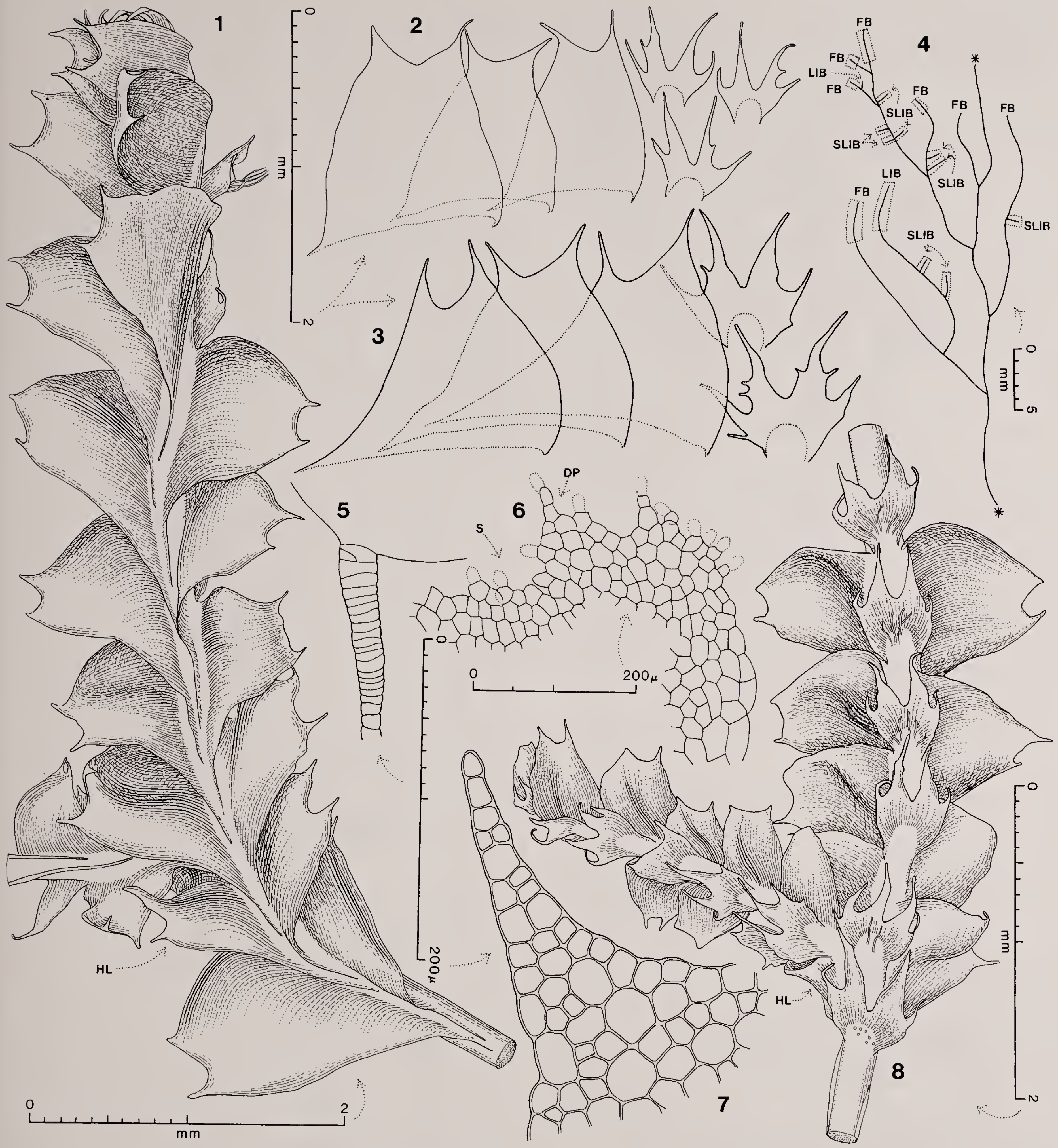


FIG. 14. *Chiloscyphus subporosus* (Mitt.) J. J. Engel & R. M. Schust. **1.** Sector of main shoot with *Frullania*-type branch (HL = half-leaf), dorsal view; note variability of leaf apex. **2, 3.** Leaves and, to right, underleaves; at top those from 1 shoot of suboptimal population, at bottom those from 1 shoot of optimal population (note variability in symmetry). **4.** Cladograph showing position of androecia (FB = *Frullania*-type branch; LIB = lateral-intercalary branch; SLIB = spicate lateral-intercalary branch that is androecial and determinate; stippled lines indicate boundaries of sectors with male bracts). **5.** Antheridium. **6.** ♂ Bract margin; note teeth in sinus (= s) between lobe and lobule; note also the distal process (= dp) and armature of free dorsal margin of lobule. **7.** Distal sector of ventral segment of leaf showing enlarged cells. **8.** Sector of main shoot with *Frullania*-type branch (HL = half-leaf), ventral view; note acute first branch leaf (oriented toward apex of main shoot). (**1, 6–8,** from *Engel 18812*, New Zealand, South Is., Mistake Cr.; **2, 4,** from *Engel 17704*, New Zealand, South Is., Morrisons Cr.; **3,** from *Engel 18806*, New Zealand, South Is., Mistake Cr.; **5,** from *Engel 18811*, same loc.)

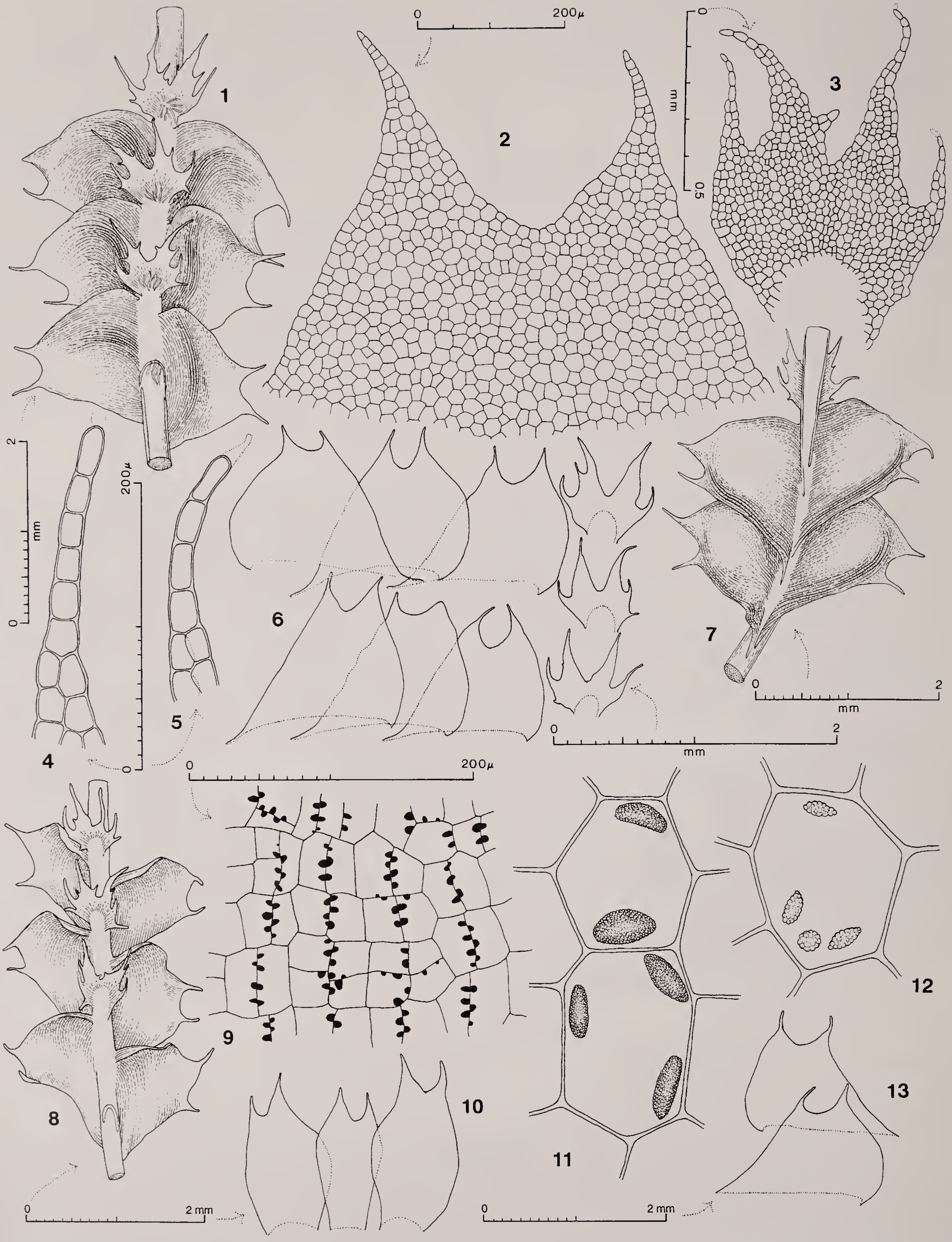


FIG. 15. *Chiloscyphus subporosus* (Mitt.) J. J. Engel & R. M. Schust. (**1–7, 9–12,** from var. *subporosus*; **8, 13,** from var. *inflexifolius*.) **1.** Sector of main, optimally developed shoot, ventral view. **2.** Distal sector of leaf showing clusters of enlarged cells and feeble development of a border at segment bases. **3.** Underleaf, note clusters of enlarged cells. **4, 5.** Distal sectors of underleaf segments. **6.** Leaves and to right, underleaves all from 1 shoot; note variability of symmetry and apex. **7.** Sector of main, optimally developed shoot, dorsal view. **8.** Sector of main shoot, ventral view. **9.** Outer capsule wall cells showing tendency toward two-phase development. **10.** ♀ Bracts and in middle, bracteole. **11.** Median cells with oil-bodies (990×). **12.** Median cells with oil-bodies (850×). **13.** Leaves. (**1, 7,** from *Engel 18806*, New Zealand, South Is., Mistake Cr.: **2–6,** from *Engel 18812*, same loc.; **8, 13,** from *Child H 425*, New Zealand, South Is., Rock and Pillar; **9,** from *Allison H6180* New Zealand, South Is., Clutha

These differences need to be evaluated carefully before merging *C. subporosus* with *C. latifolius*, and I therefore exclude the latter species from Australasia.

Schuster (1980, p. 192) stated that most reports of *C. latifolius* (= *L. bidentata*) are "open to question" and that "the numerous reports from eastern North America are at least equally dubious ... , since the taxon has been widely misunderstood." The same statement applies for reports of the species from temperate Australasia.

Hodgson (1953, p. 354) treated *C. latifolius* (= *Lophocolea bidentata*) particularly broadly by including within it the following six species that I accept: *C. subporosus*, *Heteroscyphus cuneifolius* (= *L. recurvifolia*), *C. cuspidatus* (= *L. fusca*), and three southern South American species: *C. leptanthus* (= *L. alternifolia*), *C. divaricatus*, and *C. textilis* (for comments on the American species see Excludenda, p. 203, and Engel, 1978). Hodgson also misunderstood the sexuality of the species; it is stated to be monoecious, yet her synonymy includes four dioecious plants. Allison and Child (1975) applied the name *L. bidentata* to plants that are actually *C. cuspidatus* (see sub *C. cuspidatus*, p. 54 [Note]).

As mentioned above, Hodgson (1953) recognized *L. bidentata* and differentiated the plant as having broadly ovate to subrotund leaves that are rounded to the apex. That shape is shown in her fig. 28. Hodgson (1953, p. 332) also stated that the leaves have "cells uneven (in type)," a feature that I find diagnostic for *C. subporosus*. Allison and Child (1975) also recognized the species and likewise described the leaves as broadly ovate and the apex as rather narrow (see their illustrations of the species [p. 135]). I have examined numerous collections determined as *L. subporosa* by the above three workers, who were quite consistent in their application of that name. Leaf shape, however, is more plastic than the above workers would have it. Leaves vary from asymmetrically ovate-trapezoid to ovate and then grading to very broadly ovate. Changes in symmetry often accompany this gradation—ovate trapezoid leaves are distinctly asymmetric, whereas broad ovate leaves are subsymmetric.

The ventral margin normally is entire, but the frequency of presence of a spinose tooth is variable, depending on the population. Some populations rarely and sporadically have a tooth, whereas others (e.g., *Engel 15908*) are often 1-dentate.

NOTES—1) This species has leaves with conspicuous, scattered, enlarged intramarginal cells (Fig. 15: 2). The enlarged cells are isolated, or (often) occur in clusters or rows throughout the leaf, and are present irrespective of plant vigor or development (the contrast, however, is not as distinct on leaves of smaller, less optimal shoots). The character is easily observed under the dissecting microscope, where the leaves appear speckled. No other Austral member of the genus, except large phases of *C. bispinosus*, possesses such leaf cell dimorphism, although some species, including *C. subporosus* when vigorous, have leaves and underleaves bordered by enlarged cells, at least in the vicinity of lobes.

2) Some populations (e.g., *Engel 17704* and *18812*) have exclusively *Frullania*-type vegetative branches, but both terminal and lateral-intercalary androecial branches (Fig. 14: 4). Other populations (e.g., *Engel 18221*) have both terminal and lateral-intercalary vegetative branches.

Chiloscyphus subporosus is divisible into two varieties that are separable as follows.

Key to Varieties of *Chiloscyphus subporosus*

1. Ventral margin of leaf plane, the margin oriented toward shoot apex; underleaf lamina margins plane. New Zealand, Tasmania . . . . var. *subporosus*
1. Ventral margin of leaf distinctly and broadly reflexed in basal sector and there the margin oriented toward shoot base; underleaf lamina margins reflexed. New Zealand . . . . var. *inflexifolius*

Chiloscyphus subporosus (Mitt.) J. J. Engel & R. M. Schust. var. _subporosus_

Lophocolea argentea Steph., Bull. Herb. Boissier 6(10): 874. 1906 (= Spec. Hep. 3: 99), *syn. nov. Chiloscyphus argenteus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 410. 1985 (1984). Lectotype (*nov.*): Tasmania, Mt. Wellington, Bower Creek, near Silver Falls, 28 Dec. 1897, *Weymouth 1003* (G!–c. young ♀); isolectotypes (sub no. 343): (F!, HO!).

Lophocolea petriana Steph., Bull. Herb. Boissier 6(10): 878. 1906 (= Spec. Hep. 3: 103), *syn. nov.* Lectotype (*nov.*): New Zealand, without specific loc., *Petrie 1898* (G 24407!): isolectotypes (G 24405!, G 24406!, 24411!).

Lophocolea kaalaasii Steph., Bull. Herb. Boissier 6(10): 880. 1906 (= Spec. Hep. 3: 105), *syn. nov.* Type: New Zealand, Great Barrier Is., *Kirk 440* (G!–c. per. + sporo. + ♂).

Lophocolea scorpionifolia Steph., Bull. Herb. Boissier 6(10): 883. 1906 (= Spec. Hep. 3: 108), *syn. fide* Hodgson (1953). Type: New Zealand, without specific loc., 1898, *Petrie s.n.* (G!–c ♂ + per. + sporo.).

Lophocolea beckettiana Steph., Spec. Hep. 6: 263. 1922, *syn. nov.* Type: New Zealand, South Is., Mt. Winterslow. *Beckett 496* (G!–c. per. + ♂).

Plants small to medium. Leaf ventral margin plane, not reflexed, the dorsal surface of leaf nowhere visible in ventral view of plant, the ventral margin oriented toward shoot apex. Underleaf lamina plane, not reflexed.

NOTES ON TYPE SPECIMENS—1) *Lophocolea subporosa* Mitt. The protologue lists a Sinclair collection from Auckland and a Stephenson collection from Wellington (both North Island, New Zealand). The dimorphic leaf cell character is mentioned in the protologue and illustrated in the figure of bracts and bracteole (Mitten, 1854–55, pl. XCVII, fig. 5). A well-developed perianth bearing a dorsal wing is also illustrated (fig. 4).

The Sinclair specimen has marked dimorphic leaf cells and several shoots with young gynoecia. Only one ± elongated perianth was observed; it is less mature than that illustrated in Mitten's plate (fig. 5) and has no dorsal wing.

I was able to locate only a few shoots of the Stephenson collection. Curiously the Stephenson specimen at G consists of several shoots, all sterile, whereas the specimen at FH

←

R.; **10,** from *Child 2027*, New Zealand, South Is., Frasers Gully, Dunedin; **11,** from *Engel 17704*, New Zealand, South Is., Morrisons Cr.; **12,** from *Engel 20200*, Tasmania, Mt. Wellington.)

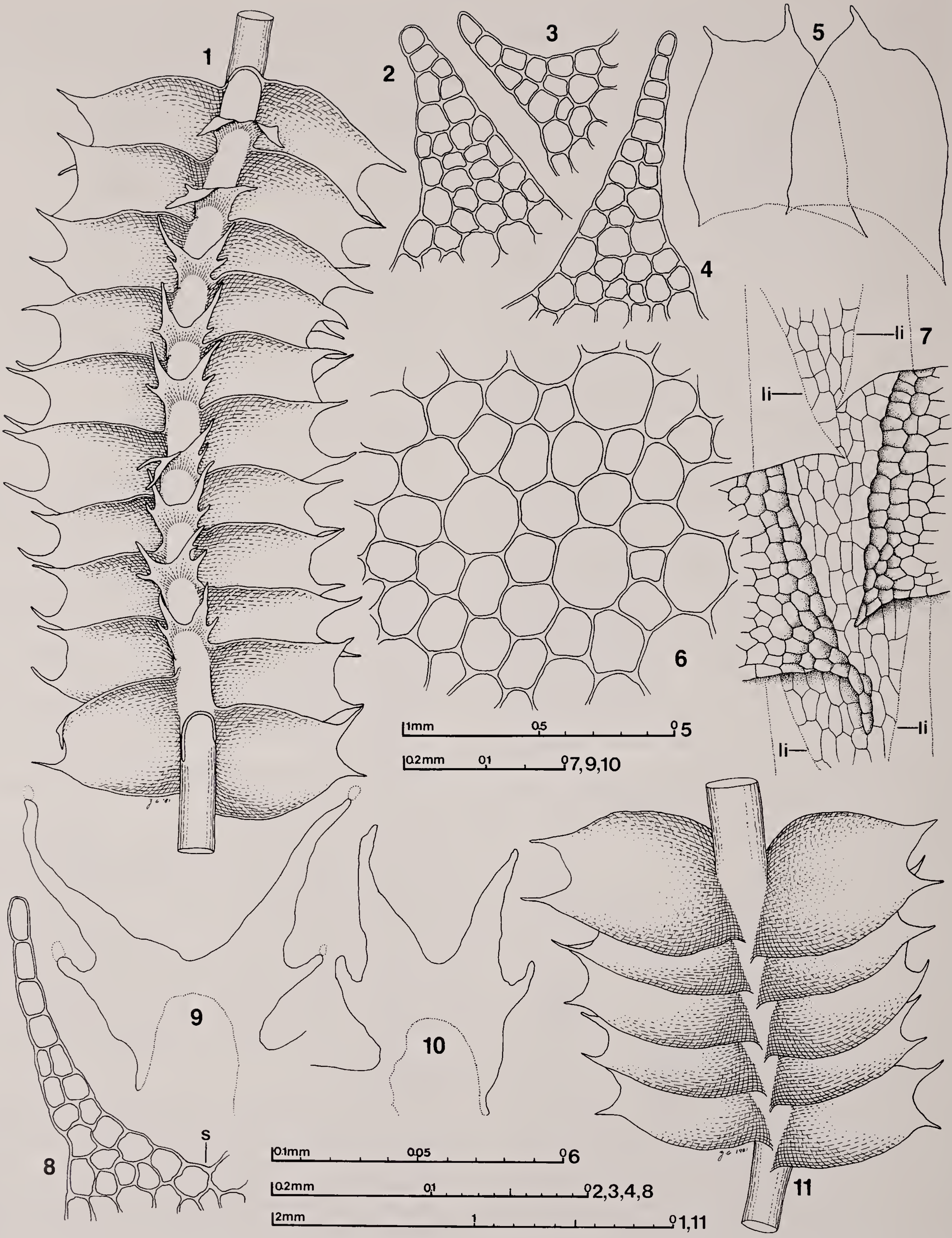


FIG. 16. *Chiloscyphus subporosus* (Mitt.) J. J. Engel & R. M. Schust. **1.** Shoot, ventral view. **2–4.** Leaf segments. **5.** Leaf outlines. **6.** Median leaf cells. **7.** Portion of stem, dorsal view, showing leaf insertion ending at stem midline (li = line of insertion). **8.** Underleaf segment (s = maximum depth of sinus). **9, 10.** Underleaf outlines. **11.** Shoot, dorsal view. (All from type [FH].)

consists of one shoot, but with a micropacket containing dissections of the perianth mouth and, presumably, bracts and a bracteole. The Stephani icon of *L. subporosa* (*Lophocolea* no. 141) is labeled "original, herb. Mitt., Stephenson" and includes perianth mouth, bract, and bracteole. The Stephenson specimen has marked dimorphic leaf cells.

I have not lectotypified *L. subporosa* because of the paucity of original material examined. No Mitten material is at NY, where one would expect to find it. The lack of Mitten original material at NY is unexplained (B. Thiers, in litt.), and perhaps such missing collections will eventually surface.

2) *Lophocolea argentea* Steph. Young gynoecia and subfloral innovations are abundant. I was able to find very few sterile, mature shoots, and on these the dimorphic leaf cell character is somewhat developed.

Specimens at G, HO, and F bear the same label information except for number. The specimen at G bears the number 1003, whereas those at HO and F have the number 343. A slip within the packet at HO reads "determ'd Stephani (sub no. 343)," and "Ex 1003"; these specimens are therefore part of the type specimen, and I have designated them as isolectotypes.

3) *Lophocolea petriana* Steph. The protologue states that the type of *L. petriana* is deposited in the Stephani herbarium. However, no specimen determined *L. petriana* at G bears label information to definitively indicate type status. Specimens bearing the name *L. petriana* at G are discussed below, with special reference to candidacy for lectotypification.

Colenso collections *(2)*—These specimens bear the collector cited in the protologue. *Colenso 1466* disagrees with the protologue in being sterile; it represents a small phase of *C. subporosus*. *Colenso 270* agrees with the protologue in several respects. Plants occur on bark, have subsymmetrically ovate leaves, and have underleaves narrowly connate on 1 side. It appears that Stephani based his icone of the species (*Lophocolea* no. 137) on this collection. The material deviates from the protologue in lacking sporophytes. The plants represent a rather small phase of *C. lentus*.

Petrie collections *(4)*—All specimens (G hb. nos. 24405, 24406, 24407, and 24411) are labeled 1898 and bear no indication of specific locality within New Zealand. All are admixed with *C. muricatus* and appear to be subdivisions of one population. The plants agree with the protologue in having 1) sporophytes with nondehisced capsules (because a capsule shape is provided in the protologue, at least some must be nondehisced); 2) marked dimorphic leaf cells (i.e., cells "ubique valde irregulares" in the protologue); 3) perianths deeply 3-lobed at the mouth; and 4) a bark substrate. They disagree with the protologue in having rather asymmetrically ± deltoid leaves and free underleaves. This population represents well-developed *C. subporosus*.

Beckett 241—The material bears no sporophytes; it is referable to *C. lentus*.

Kirk 556—The specimen bears no sporophytes; it is referable to *C. subporosus*.

It is apparent that Stephani's description of *L. petriana* is a composite of two elements represented by *Colenso 270* and *Petrie 1898*. The sporophyte-bearing population (leg. Petrie) is designated as lectotype of *L. petriana*.

4) *Lophocolea kaalaasii* Steph. The specimen consists of abundant gynoecium-bearing shoots and subfloral innovations; I was able to locate only a few sterile shoots. The fertile and sterile shoots have quite different underleaf characters, and discrepancies are germane to disposition of the species. Sterile shoots match those subfloral innovations that do not culminate in archegonia formation. Such shoots have underleaves that are free, divided nearly to the base, and have a prominent lacinia on each side of the lamina. These characters agree with the protologue and the illustration of the underleaf in the Stephani icones (*Lophocolea* no. 132). All other shoots bear gynoecia of varying stages—some mature and bearing sporophytes, others in early leaf fusion stages. Still others are presumably gynoecial (underleaves and leaves increase in size and underleaves decrease in sinus depth toward the shoot apex), but archegonia are difficult to demonstrate or the shoot tips are missing. Gynoecial shoots have underleaves concave, ca. 0.4–0.5-fid, with lamina margins entire or 1-dentate. Innermost bracteoles are free. Leaves are consistently short bifid, trigones are small and dimorphic leaf cells feebly developed.

Hodgson (1953, p. 355) stated that "the packet labeled *L. kaalaasii* was Kirk's No. 440. It is similar to *L. grandistipula* Schiffn. and *L. kirkii* St., varietal forms of *L. novae-zelandiae* (sic)." This conclusion is understandable, if it is based solely on gynoecial shoots. I have placed the species in the synonymy of *C. subporosus* on the basis of character states of both sterile and gynoecial plants.

5) *Lophocolea scorpionifolia* Steph. The plants are flaccid and closely appressed to the bark substrate. The specimen has abundant androecia and perianths, as well as a few capsules (the last not indicated in the protologue). The androecia often are elongate and may be composed of up to 14 bract pairs. Androecia and gynoecia are intimately intermixed, but I found no evidence of physical connection. Leaves are subsymmetric, the dorsal margin is straight or nearly so and ± decurrent on the stem, whereas the ventral margin is somewhat arched. The ventral margin is mostly entire, but occasionally has a spinose tooth. Leaf lobes terminate in a uniseriate row of 5–7 cells. Underleaves are free and divided nearly to the base. The scattered enlarged cell character is difficult to demonstrate on this specimen. The feature is expressed, though feebly, on some of the larger shoots, but such shoots often are in poor condition and have incomplete leaves. The perianths are rather deeply lobed, and each lobe has acuminate segments with margins sparingly spinose dentate or, sporadically, entire. The specimen represents a rather small, relatively weak phase of *C. subporosus*—the small plant size, subsymmetric leaves, and reduced underleaf lamina support this.

6) *Lophocolea beckettiana* Steph. The specimen consists of two micropackets: one containing a small piece, the other several shoots. Nearly all shoots bear either perianths or androecia. Leaves are ± subsymmetric, uniformly entire margined, and the lobes terminate in a uniseriate row of 4–7 cells. The dorsal margin is ± straight and long-decurrent on the stem. Underleaves are free, although the margin on one side is in close juxtaposition to the ventral base of the adjoining leaf. The underleaves are bifid nearly to the base, and the lamina on each side has a laciniiform process. Most leaf cells are small, but scattered among them are enlarged cells. Trigones are small and concave sided. The perianth is shallowly to rather deeply lobed, and each lobe has medium acute to acuminate segments with margins entire or sparingly spinose dentate. The protologue states the plant was terricolous, and I find no evidence to dispute this. The specimen represents a rather weak phase of *C. subporosus*—

small plants, subsymmetric leaves, and reduced underleaf lamina support this. Stephani erroneously spells the collector's name "Buckett."

Distribution—Confined to Australasia, the species occurs on Auckland Is., New Zealand (Stewart Is.; South Is., sea level–1795 m; North Is., sea level–680 m), Snares Is., Antipodes Is., Australia: Tasmania (sea level–1280 m), A.C.T. (50–760 m), New South Wales.

Ecology—The variety has a rather broad ecological amplitude throughout its range. In New Zealand forests it is rather commonly associated with wood and occurs, for example, on rotted, old logs, fallen tree trunks or branches, bark of upright trees and shrubs (*Fuchsia*, and others) and tree roots. Niches grade from damp, shady situations to rather open bush. In shaded forest sites it also occurs on earth or soil over rocks in a variety of niches, sometimes on banks in gullies, sometimes on the banks of watercourses. In more open sites it may occur, for example, in a mosaic of boulder fields and ferns with patches of mixed *Nothofagus menziesii* forest (Fiordland Natl. Park, Mistake Creek, *Engel 18812*). At this site, the variety is found on bark of exposed small trees in the boulder field. It also occurs in coastal situations on rocky (sometimes limestone) banks, sheltered by woody vegetation. For example, at Ti Point Scenic Reserve (south of Leigh, North Auckland Prov., *Engel 20291*) the variety occurred in coastal forest remnants dominated by *Metrosideros excelsa* and *Vitex lucens* and was found on a thin layer of soil over a boulder. On the other hand, the variety may be present in quite exposed coastal sites, such as on sandy, open flats on the banks of Akatore Creek (at the creek mouth, south of Dunedin, leg. *Allison H1374*). It tolerates other exposed conditions as well; for example, on tussock bases in low windswept vegetation consisting mainly of *Bulbinella* and *Festuca novae-zelandiae* (leg. *Engel 17714* in the Kakanui Mtns., Otago Prov. at a relatively dry site with few other hepatics present). The variety is rare in subalpine–alpine sites and may be found in crevices of rocky outcrops or at streamsides.

The variety also is able to tolerate disturbed sites of various sorts; several examples follow. It may occur on soil and concrete at the base of concrete walls on a grazed slope dominated by native and introduced grasses (Canterbury Prov., leg. *Fife 5608*), as well as on concrete of building foundations and culvert walls. It also may be found in roadside ditches or grassy patches, on earth under willows or pines, as well as on prostrate willow trunks. The variety also occurs in forest remnants subject to some disturbance; it is present, for instance, in the Dunedin Botanical Garden.

Variety *subporosus* has a similar ecology in Tasmania. In forests it occurs on very rotted wood or on soil over boulders in *Eucalyptus* forests of varying density. In mosaics of boulder fields and scattered patches of *Eucalyptus*, it occurs between boulders (particularly where some soil has accumulated) in boulder fields. In the subalpine–alpine zone, the variety occurs in protected niches, such as terrestrial or on soil over rock under shrubby cover, between boulders in boulder fields, in vertical crevices of cliffs.

The variety may be present in more exposed sites, occurring, for example, on *Eucalyptus* bark in dry button grass plains with patches of open *Nothofagus* and *Eucalyptus* forest (shore of Lake Lea, *Norris 27469*). The variety tolerates disturbed sites, such as a stump in a burned-over *Eucalyptus* forest, or exposed soil of a roadside in a cut-over *Eucalyptus* forest, or in a grazed creek valley in an open *Eucalyptus* forest (occurring on *Salix* bark).

The variety appears to frequent lower to medium-level rainfall levels but is intolerant of high rainfall levels. In New Zealand the species is lacking in the wet southwestern and western sectors of South Is., and in Tasmania the species is rather common in the eastern and northern sectors, sporadic in the west, and altogether lacking in the southwest.

Specimens Seen (selected)—**AUCKLAND IS.:** French Islet, Port Ross, *Fineran 1588* (CHR); No. 2 Camp, *Turbott H51* as *L. lenta* (CHR). **NEW ZEALAND. STEWART IS.:** Mutton Bird Is., Stage Is., *Fineran 115* (CHR). **SOLANDER IS.:** SE peninsula, 100–110 m, *Johnson s.n.* (CHR); SE ridge, 130 m, *Johnson s.n.* (CHR). **SOUTH ISLAND. SOUTHLAND:** 20 mi. NW of Riverton, ca. 150 m, *Child H 1639* as *L. bidentata*–c. per. (F); Garvie Range, East Dome, ca. 1370 m, *Child H 3909* (F); Fiordland Natl. Park, near outlet of Lake Te Anau, ca. 205 m, *Allison H 1408* a *L. decurrens*–c. ♂ (CHR); ibid., Central Earl Mtns., Mistake Creek, between Triangle Peak and Melita Peak, NE of N end of Lake Te Anau, 740–800 m, *Engel 18812*–c. ♂ (F). **OTAGO:** Clutha River, near Kaitangata, *Allison H 6180*–c. sporo., *6340* (CHR); Akatore Stream, S of Dunedin, *Allison H 1374* as *L. decurrens*, *H 1407* (CHR); road from Akatore to Waihola, ca. 150 m, *Simpson s.n.* as *L. bispinosa* (CHR); Lake Waihola, SW of Dunedin, sea level–15 m, *Child H 159* as *L. bidentata*–c. per. (F); near Berwick, S of Dunedin, *Allison H 1343* as *L. decurrens* (CHR); Berwick State Forest, S of Dunedin, *Allison H 1397* as *L. decurrens* (CHR); Waipori River Gorge, S of Dunedin, *Allison H 1378* as *L. lenta* (CHR); Dunedin Botanic Gardens, ca. 15–30 m, *Child H 604* as *L. lenta*–c. ♂, *H 609* as *L. dalliana* (F); Dunedin, Town Belt, ca. 150–215 m, *Child H 1333* as *L. bidentata*–c. ♂, *H 1406* as *L. lenta*, *H 1407* as *L. decurrens* (F); ibid., Cosy Dell, ca. 150–215 m, *Child H 1510*–c. sporo., *H 1648* as *L. bidentata* (F); ibid., Frasers Gully, ca. 60–90 m, *Child H 2027* as *L. lenta*–c. per. + ♂ (F); Mt. Charles, ca. 365 m, *Child H 293* as *L. insularis*, *H 304* as *L. bispinosa*–c. ♂ (F); Leith Valley, near Dunedin, ca. 90 m, *Child H 64* as *L. bidentata* (F); Morrisons Creek, N of Dunedin, 330 m, *Engel 17704*–c. ♂ (F); Ross Creek, Dunedin, ca. 150–185 m, *Child H 2354*–c. sporo. + ♂ (F); Lee Stream, ca. 305 m, *Child H 2506*–c. sporo. (F); ibid., Hindon Road, ca. 305 m, *Child H 895* as *L. decurrens*, *H 902*–c. per. (F); Mt. Cargill, Dunedin, *Allison H 4685* as *L. lenta* (CHR); Mopanui, N of Dunedin, ca. 305 m, *Child H 1370* as *L. semiteres* (F); Waitati, near Dunedin, sea level, *Simpson et al. s.n.* (CHR); Hindon, ca. 455 m, *Child H 1030* as *L. lenta*–c. ♂ (F); Mt. Pleasant, ca. 455 m, *Child H 264* (F); Horse Range Road, N of Palmerston, 90–120 m, *Allison H 1404* as *L. decurrens* (CHR); Alexandra, Frasers Gully Domain, ca. 305 m, *Child H 1430* (F); Maheno, sea level, *Child H 134* as *L. lenta*–c. sporo. (F); Longlands Station, Maniototo, ca. 455 m, *Child H 3934* (F); Kakanui Mtns., summit of Pigroot, off Hwy 85 between Kyeburn and Morrisons, 710 m, *Engel 17714* (F); Kakanui Range, ca. 915 m, *Child H 2826* as *L. inflexifolia* (F); Queenstown Garden, ca. 365 m, *Allison H 6795* (CHR); Pierce Creek, Falls Dam, ca. 610 m, *Child H 857* as *L. lenta* (F); Paradise, Jordan River, head of Lake Wakatipu, ca. 365–455 m, *Child H 103*, *H 1216* as *L. lenta* (F); ibid., Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, *Child H s.n.121* (F); Rees Valley, Invincible Creek, ca. 455 m, *Child H 378* as *L. decurrens* (F); Mt. Aspiring Natl. Park, Blue River near confluence with Makarora River, NNE of Makarora, 310 m, *Engel 18907*–c. ♂ (F). **WESTLAND:** Haast Pass, near Pleasant Flat, *Allison H 6798* (CHR); Open Bay Is., Taumaka, off Haast-Jackson's Bay coast, *Horning 316* (CHR). **CANTERBURY:** Arowhenua Homestead, W of Temuka, *Macmillan 77/230A*, *77/232A*, *77/241* (CHR); Peel Forest, ca. 150 m, *Child H 2085* (F); Banks Peninsula, Price's Valley, ca. 60 m, *Macmillan 77/212A* (CHR); ibid., Akaroa Harbour, Wainui, *Macmillan 76/377* (CHR); ibid., Reynolds Valley Road, ca. 1 km below junction with Bossu Road, ca. 630 m, *Fife 6839* as *L. bidentata* (F); ibid., Packhorse Track, SW of Mt. Herbert, *Macmillan 77/276* (CHR); ibid., Port Hills, Dry Bush, ca. 305 m, *Macmillan 75/66* (CHR); "Sugarloaf Bush," Cass Field Station, 700–800 m, *Fife 6750* (F); Lake Ellesmere, S of Christchurch, sea level, *Child H 1418* as *L. bispinosus* (F); Mt. Cook Natl. Park, Governors Bush, SW of town of Mt. Cook, 760–800 m, *Engel 18221* (F); Port Hills, S slope of Godley Head, sea level–500 m, *Fife 5608* (F); Christchurch, Waimairi Road, *Macmillan 77/188* (CHR); ibid., Riccarton Bush, *Macmillan 76/401*, *76/409* as *L. lenta* (CHR); Ashley River Bridge, N of Rangiora, 30 m, *Macmillan 74/56* (CHR); Onepunga, NE side of Mt.

Grey, ca. 365 m, *Macmillan 80/39* (CHR); Ngawiro, Waiau, N end of Lowry Peaks Range, ca. 305 m, *Macmillan 80/10* (CHR). **NELSON:** Cape Foulwind, W of Westport, ca. 30 m, *Child H 3601* (F); Matiri Range, *Brown s.n.*–c. ♂ (AK); Mt. Arthur, ca. 1580–1795 m, *Brown 88/36e* as *C. lentus*, *88/50* as *L. bispinosa* (AK); Mt. Arthur Tableland, ca. 1220 m, *Child H 3787* (F); Arthur Range, S flank of Hoary Head, 1300–1320 m, *Fife 7541* (F); ibid., summit plateau of Hoary Head, 1390–1440 m, *Fife 7509* (F). **MARLBOROUGH:** Wairere Stream, S of Kaikoura, *Lewinksy 74-512* a *L. bidentata*, *74-528* as *L. lenta* (CHR); Red Hills, ca. 915 m, *Child H 4379* (F); Waihopai Valley, ca. 305 m, *Child H 3449* (F); Kaiuma, Pelorus Sound, NNE of Havelock, ca. 5 m, *Child H 4459* (F); Cook Strait, Stephens Island, *Macmillan 71/222*, *71/273* as *L. lenta* (CHR). **NORTH ISLAND. WELLINGTON:** Wiltons Bush, *Mason s.n.*–c. ♂ + sporo. (CHR); near Martinborough, Wairarapa, *Mues NZ 46* (F); Manawatu Gorge, *Zotov s.n.* (CHR); S Ruahine Mtns., *Druce 762*–c. ♂ (CHR); Wanganui, near St. John's Lake, *Whitehouse 29812* (F). **HAWKE'S BAY:** Mahia Peninsula, Pongaroa, *Sainsbury s.n.* (CHR); near Wairoa, *Hatcher 1284* (F); Morere, *Hatcher 21* as *L. lenta* (F); Poverty Bay, Panikau, *Sainsbury s.n.* (CHR). **GISBORNE:** Waikaremoana, *Butler 2152* (CHR). **TARANAKI:** Mokauiti Valley, 20 mi. S of Te Kuiti, ca. 455 m, *A. Allison s.n.* (CHR). **SOUTH AUCKLAND:** Roto-a-kui Bush, E of Taupo, ca. 670 m, *Allison H 3423* (CHR); Whirinaki State Forest, "Cathedral Grove Track," E of Lake Taupo, *Braggins s.n.* as *L. decurrens* (AK); Kaingaroa Plains, Rotorua region, *Allison H 3404* (CHR); Kaingaroa State Forest, Rotorua region, *Allison H 3425* as *L. bidentata*–c. ♂ (CHR); Pureora, W Taupo, near Pikiariki Road, off Fury Road, *Braggins s.n.* as *L. lenta* (AK); Broadlands, S of Rotoroa, 305 m, *Child 1415* as *L. lenta*–c. ♂ (F); E of Waiotapu Valley, ca. 520 m, *Allison H 3422* as *L. bidentata*–c. ♂ (CHR); Waikato River, Ongaroto Road, near Atiamuri, S of Rotorua, *Allison H 3368* (CHR); ibid., below Atiamuri, S of Rotorua, *Allison H 3378* as *L. novaezeelandiae*–c. per. (CHR); Rotoroa, Taupo Road, ca. 305 m, *Child H 44* (F); between Lake Rotoehu and the coast, Bay of Plenty, *Allison H 3494* (CHR); Mangorewa Gorge, Matai Road between Rotorua and Te Puke, *Allison H 3363* (CHR). **NORTH AUCKLAND:** Waitakere, ca. 60–150 m, *Child H 2233* (F); Mt. Eden, Auckland, *Braggins s.n.* (AK); Auckland, Government House, *Macmillan 76/319* (CHR); ibid., University of Auckland, *Braggins s.n.* as *L. bidentata* (AK); Woodhill Forest, Pukitu, 100 m, *Cameron 4607* as *L. bidentata* (AK); Track to Ti Point Scenic Reserve, N head of Whangateau Harbour, S of Leigh, edge of sea, *Engel 20291* (F); Waima Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, 650–680 m, *Engel 22591* (F); E Cauldron Bay, Mokohinau Is., Fanal Is., *Cameron 2734c* (AK); Hen and Chickens Is., Middle Stack, *Beever 9-98f* (AK); Three Kings Is., SW island, ca. 160 m, *Cameron 2422* (AK). **LITTLE BARRIER IS.:** Te Titoki Point, *Braggins et al. 80/990b* (AK); N of Te Titoki Point, *Braggins et al. 80/266* as *L. bidentata* (AK). **SNARES IS.:** SW promontory, *Horning SA 46* (CHR); near arm of Ho Ho Creek, *Horning SA 71* (CHR). **ANTIPODES IS.:** Reef Point, ca. 15 m, *Godley s.n.* as *L. bidentata*–c. ♂ (CHR); near Reef Point, *Godley s.n.* as *C. physanthus* (F). **TASMANIA.** Bruny Is., Adventure Bay, *Rodway s.n.* as *L. bispinosa* (HO); Tasman Peninsula, Port Arthur, *Weymouth 622* as *L. austro-alpina* (HO); ibid., Newman's Creek, *Weymouth 614* as *L. bispinosa* (HO); Iron Creek near Tier Gully about 7 mi. S of Nugent on road to Sorell, ca. 150 m, *Norris 30463* (F); Burns Creek, ca. 200 m, *Norris 30788* (F); Freycinet Natl. Park, trail to Wineglass Bay, ca. 100–400 m, *Norris 30620* (F); Sassafras Gully, ca. 490 m, *Ratkowsky s.n.*–c. sporo. (F); Mona Vale, near Ross, *Weymouth 859* as *L. bispinosa* (HO); summit area of Mt. Barrow, ENE of Launceston, 1300 m, *Engel 15231* (F); St. Patrick's Head, ca. 610 m, *Weymouth 1244*, *1247*, both as *L. mooreana* (G), *1244* as *L. lenta*–c. ♂, *1249* as *L. fissistipula*, *1252* as *L. decolorata*–c. sporo. (HO); St. Mary's Pass, The Glen, ca. 275 m, *Weymouth 1254* as *L. multipenna*, *1255* as *L. longistipula* (M); Blue Tier, *Rodway s.n.* as *L. lenta* (HO); Legerwood Creek, at Scottsdale to St. Helens Highway, *Norris 31947* (F); Launceston, Cataract Gorge, *Weymouth 1306* as *L. subemarginata* (HO); Great Taylor's Bay, *Rodway s.n.* as *L. variabilis* (HO); Sandfly, *Rodway s.n.* as *L. austro-alpina* (HO); Fern Tree, near Hobart, *Ratkowsky s.n.*–c. per. + ♂ (F), *79/96* (HO); trail from Fern Tree to Silver Falls, ca. 500 m, *Norris 29191* (F); Wellington Falls Track, ca. 760 m, *Ratkowsky s.n.* (F); Mt. Wellington, *Ratkowsky s.n.* as *L. lenta* (F); ibid., *Rodway s.n.* as *L. lenta* (HO); ibid., NW Bay River, bottom of Pipeline Track, *Ratkowsky 78/137*–c. ♂ (HO); ibid., St. Crispins Well, *Ratkowsky s.n.* (F); ibid., S slope, upper Pipeline Track, E of St. Crispins Well, 750 m, *Engel 20200*–c. ♂ (F); ibid., Watchorn's Creek, *Weymouth 96* as *L. austro-alpina* (HO); ibid., Deep Creek (= Long Creek), *Weymouth 493* as *L. bispinosa* (HO); ibid., Deep Creek Track, ca. 490 m, *Weymouth 493* as *L. bridelii* (HO); ibid., Deep Creek near Trolley Hut., ca. 535 m, *Weymouth 511* as *L. austro-alpina* (F, HO); ibid., Silver Falls Pipeline, 600 m, *Ratkowsky 77/159* (HO); ibid., The Springs Track, ca. 610 m, *Weymouth s.n.*, *1529*, both as *L. austro-alpina* (HO); ibid., near Junction Cabin, 600 m, *Ratkowsky 77/156* (HO); ibid.,Guy Fawkes Rivulet, *Rodway s.n.* as *L. bidentata*, *s.n.* as *L. variabilis* (HO); ibid., ibid., *Weymouth 470* as *L. bispinosa* (HO); ibid., Myrtle Gully, *Ratkowsky s.n.*–c. sporo. (F), *78/134* (HO); ibid., summit plateau, 1280 m, *Engel 16370* (F); Collins Bonnet, 1000 m, *Ratkowsky s.n.* (F); Kingston, *Ratkowsky s.n.* (F); Kingston Beach, *Ratkowsky s.n.* (F); Kingston Beach Track, sea level, *Ratkowsky 78/128* (HO); Fire Roads, Knocklofty, *Ratkowsky s.n.*–c. sporo. (F); Huon Road, near Hobart, ca. 455 m, *Ratkowsky 77/150*–c. ♂ (HO); Hobart Rivulet, *Weymouth 241* as *L. bispinosa* (HO); Headrace Reservoir, Hobart, *Rodway s.n.* as *L. austro-alpina* (HO); Brushy Hill, 250 m, *Ratkowsky 77/161*–c. ♂ (HO); New Town Rivulet, near Hobart, *Weymouth s.n.* as *L. lenta* (HO); ibid., Augusta Road, near Hobart, *Weymouth 719* as *L. bispinosa* (HO); Mt. Field Natl. Park, *Ratkowsky 78/142* (HO); ibid., Lake Webster, *Ratkowsky 80/74* (HO); ibid., track to Lake Fenton, *Rodway s.n.* as *L. bispinosa* (HO); along Styx River Road at crest of ridge about 4 mi. S of Gordon River Road, *Norris 28996* (F); Great Lake, *Rodway s.n.* as *L. macroloba* (HO); ibid., S end, at intersection of road to Bronte Park, ca. 1100 m, *Norris 33045* (F); ibid., at Headrace Tunnel, ca. 1100 m, *Norris 32462* (F); Great Western Tiers, vicinity of Devils Gullet Lookout, above Fisher River and W of Lake Mackenzie, 1140 m, *Engel 15908* (F); Lake Lea, ca. 800 m, *Norris 27469* (F); ridge SE of Black Bluff near junction of access road to plateau area and road to Devonport gold mines, S of Burnie, 1000 m, *Engel 16222* (F); West Downs, terminus of Basils Road, SSW of Burnie, 575 m, *Engel 15872* (F); Lyons Creek, about 3 mi. W of Liena, ca. 700 m, *Norris 32690* (F); summit area of Mt. Roland, just E of Gowrie Park, 1160–1200 m, *Engel 20132*–c. ♂ (F). **AUSTRALIA. A.C.T.:** Bimberi Range, 49 km SW of Canberra, *Streimann 4419* (CBG); Blue Range, near Musk Creek crossing on Pabral Road, near Blundell's Flat, 760 m, *Curnow & Lepp 340* as *L. pallida* (NY); National Botanic Gardens, Canberra, 650 m, *Streimann 7777* (CBG). **NEW SOUTH WALES:** Orange, *Wilson s.n.* as *L. austro-alpina* (G).

Chiloscyphus subporosus* var. *inflexifolius (Steph.) J. J. Engel

> *Lophocolea inflexifolia* Steph., Spec. Hep. 6: 278. 1922. *Chiloscyphus inflexifolius* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 417. 1985 (1984). *Chiloscyphus subporosus* var. *inflexifolius* (Steph.) J. J. Engel, Phytology 83: 45. 1998 (1997). Type: New Zealand, Pain's Limestone Hill, Wairarapa, 28 Nov. 1910, *Gray 209*, ex hb. Rev. Lillie (G!).

Plants robust. Leaf ventral margin reflexed in basal sector, a portion of dorsal surface of leaf visible in ventral view of plant, the basal sector of ventral margin oriented toward shoot base; underleaf lamina margins somewhat reflexed.

DIFFERENTIATION—This variety represents a particularly robust phase of the species. Such plants approach large phases of *C. bispinosus* and therefore may offer confusion. The two taxa, for example, have acuminate to subcaudate leaf lobes, reflexed ventral leaf margins (basal sector), somewhat reflexed underleaf disc margins and a well-defined border of enlarged cells of both leaf and underleaf. The following suite of diagnostic characters preclude placement in *C. bispinosus*: the leaves are bifid to 0.2–0.3, have plane lobes, and usually entire ventral margins (only sporadically with a spine); the underleaf lamina is 6–14(19) cells high; and trigones are minute or small. Furthermore, the leaves have a particularly pronounced speckled appearance because of the distinctly dimorphic cells.

The appearance of the robust extreme in ventral aspect is reminiscent of the sparsely armed variant of *C. villosus*, particularly with regard to recurved ventral leaf margins and underleaf form (compare Figs. 15: 4 and 76: 3). Polymorphic leaf apices will immediately distinguish that phase of *C.*

villosus. Only smaller, weak, often flaccid plants of *C. subporosus* have polymorphic leaf apices.

Hodgson (1953) and Allison and Child (1975) recognized this phase as *L. inflexifolia* Steph. These authors used the reflexed ventral margin of the leaf in their keys and noted the dimorphic leaf cells.

VARIATION—Length and degree of reflexation of the ventral margin of the leaf is variable. Optimally it is broadly reflexed in the basal half of the margin; this condition is present in the type of *L. inflexifolia* (see below). In less optimal plants the margin is reflexed only at the extreme base, with merely a narrow strip of dorsal surface of leaf exposed in ventral view.

NOTES ON TYPE SPECIMENS—1) *Lophocolea inflexifolia* Steph. Leaves are long decurrent dorsally, have the uniseriate row of lobes composed of 5–7 cells, and have the ventral margin of the leaf in its basal half broadly reflexed, such that the dorsal surface of the leaf is partially in view and the ventral margin is aligned toward the shoot base. The leaves have a pronounced speckled appearance because of the scattered enlarged cells among markedly smaller ones. Trigones are lacking. Underleaves are similar to the Stephani Icon of the species (*Lophocolea* no. 130) except the lobes are piliform distally and have a long uniseriate row of cells. Underleaf lobes are armed with cilia, and the lamina on each side has an accessory caudate lobule. The plants represent the robust extreme of the species except for the uniformly low underleaf lamina, being only 3–4(7) cells high.

DISTRIBUTION AND ECOLOGY—Known only from a limited suite of collections in New Zealand: a few scattered sites on South Is. and two sites on North Is., the type (Wairarapa) and the Urewera Natl. Park station; it is also present on Chatham Is. The var. *inflexifolius* on the whole occurs at elevations higher than those of var. *subporosus* and is absent below 610 m on South Is. and on North Is. occurs at 930–1030 m, the only recorded elevation for that island. At Rainbow Skifield (Nelson) the variety occurs at 1360–1480 m on soil over boulders in a mosaic of tussock grass and alpine vegetation along with tarns, rills, rocky outcrops, and boulder fields. Below the ski field, at 1210 m, the variety is present in the uppermost reaches of a *Nothofagus solandri* var. *cliffortioides* forest, occurring on a vertical rock face at the margin of a stream in a steep-sided, narrow valley with nearly vertical cliff-like sides. On the track to the Whakataka summit in Urewera Natl. Park the variety was found on a thick soil layer over a bryophyte covered log in a *Nothofagus fusca-N. menziesii* forest.

SPECIMENS SEEN—**NEW ZEALAND. SOUTH ISLAND. OTAGO:** Blue Mtns., ca. 915 m, *Child 387* (F); Rock and Pillar, 760–1280 m, *Child H 425*, *H 3028* (F); Herbert, Breakneck Road, ca. 610 m, *Child 288* (F); vicinity of Quartz Reef Hill, ca. 915 m, *Allison H 5724* (CHR). **NELSON:** Nelson Lakes Natl. Park, St. Arnaud Range, Arnst Basin, ca. 1740 m, *Simpson 4023*, *4026* (CHR); St. Arnaud Range, Rainbow Skifield, S of St. Arnaud, 1360–1480 m, *Engel 22775* (F); ibid., Rainbow Skifield just below ski tow area, S of St. Arnaud, 1210 m, *Engel 22812* (F). **NORTH ISLAND. NEAR GISBORNE/SOUTH AUCKLAND BOUNDARY:** Urewera Natl. Park, crest trail from Highway 38 toward Whakataka summit, N of northern extremity of Lake Waikaremoana, 930–1030 m, *Engel 20663* (F). **CHATHAM IS.:** Crispans Lane, Orihou Stream, ca. 10 m, *de Lange CH1043* (AK, F).

Chiloscyphus cuspidatus (Nees) J. J. Engel & R. M. Schust.

Lophocolea bidentata var. ß *cuspidata* Nees, Naturg. Eur. Leberm. 2: 327. 1836. *Lophocolea cuspidata* (Nees) Limpr. *in* Cohn, Krypt.-Fl. Schlesien 1: 303. 1876. *Chiloscyphus cuspidatus* (Nees) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 413. 1985 (1984). Type: Germany, Riesengebirge, *von Flotow*.

Lophocolea setacea Steph., Hedwigia 31: 125. 1892, *syn. fide* Jones (1953). Type: South Africa, "prope Clermont. leg. Rehmann."

Lophocolea longispica Steph., Hedwigia 31: 210. 1892, *syn. fide* Jones (1953). Type: Mascarene Is., Rodriguez.

Lophocolea fusca Steph., Bull. Herb. Boissier 6(10): 872. 1906 (= Spec. Hep. 3: 97), *syn. nov.* Type: New Zealand, without specific loc., *Colenso 1931 p. p.* (G!–c. ♂ + per. + sporo.).

Lophocolea mooreana Steph., Bull. Herb. Boissier 6(10): 875. 1906 (= Spec. Hep. 3: 100), *syn. nov. Chiloscyphus mooreanus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 419. 1985 (1984) (*non Chiloscyphus moorei* Steph., Hedwigia 33: 2. 1894 [= *Heteroscyphus*]). Lectotype (*nov.*): Tasmania, Jones Track, 17 Sept. 1895, *Moore s.n.* (G 024458!–c. ♂ + per. + sporo.).

Lophocolea scott-elliottii Steph., Bull. Herb. Boissier 7(4): 308. 1907 (= Spec. Hep. 3: 172), *syn. fide* Jones (1953). Type: Uganda, "in monte Runssoro (= Ruwenzori) (*Scott Elliott*)."

Leptoscyphus stephensii Sim, Trans. Roy. Soc. South Africa 15: 105. 1926, *syn. fide* Arnell (1955). Type: South Africa, "Table Mountain, Miss Stephens (Sim n. 9527, 9528); Stellenbosch (Sim n. 9529)."

Lophocolea arisancola Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 169. *f. 22*. 1934. Holotype: Taiwan, Mt. Arisan, (Numanodaira-Iwaiyama), Prov. Tainan, Aug. 1932, *Horikawa 11075*.

Lophocolea cuspidata subsp. *antipodea* R. M. Schust., Hep. Anthoc. N. Amer. 4: 203. 1980, *syn. nov.* Holotype: New Zealand, South Is., Mt. Cook Natl. Park, Sealy Range, above Sealy Lakes, ca. 5200 ft, *Schuster 67-491a* (F!).

Plants rather flexuous, very loosely growing over substratum and prostrate to ascending, very pale and hyaline green; shoots often quite flat in dorsal view, when well developed 3–4 mm wide, smaller phases 2.6–3 mm wide. Branches frequent, of *Frullania* type (the half-leaf undivided and with the apex similar to a leaf lobe, or if divided [rare], then the ventral lobe much larger and the dorsal lobe appearing as a process on the dorsal margin); lateral-intercalary branches variable in frequency: in some populations sporadic while terminal branches are common, in others of equal frequency to terminal branches. Stems narrow for plant size, 10–11 cells high, the cortex moderately differentiated, in 1(2) layers of cells somewhat smaller than those of medulla, the cortical and medullary cells thin walled except for the slightly thickened exposed walls of cortex. Rhizoids in tight fascicles from stem at immediate base of underleaves, the rhizoids short for plant size. Leaves alternate, usually horizontal, widely spreading, mostly loosely imbricate but occasionally densely so, free dorsally, the orientation strongly succubous, the insertion distinctly recurved at ventral end (weakly to distinctly J-shaped), the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves broadly and rather evenly convex, a- to subsymmetrically ovate-trapezoid to trapezoid, occasionally subsymmetrically ovate, length/width ratios variable: ranging from 1.3× wider than long to 1.6× longer than wide, widest near base, apex bifid to 0.2–0.35(0.45), the lobes parallel to diverging, plane, the ventral often considerably larger, subcaudate, tapering from a narrowly to broadly acute basal sector to a zone of up to 7 tiers of 2 laterally juxtaposed cells and, ultimately, terminating in a piliform tip consisting of a uniseriate row of 5–10(13) cells that are variable but usually longer than wide, being 12–23 µm wide × 22–40 µm long or 1.3–2.2× longer than wide and only rarely and sporadically isodiametric, the lobe margins entire, the sinus broadly rounded to lunate, the sinus + lobe margins often delimiting a half circle; dorsal margin straight to broadly and evenly slightly arched, plane to somewhat deflexed, entire, often very long decurrent; ventral margin broadly arched (sharply so at base), slightly to distinctly more arched than the dorsal, plane to sharply deflexed in basal sector, entire or sporadically with 1(2) ciliiform projections. Leaf cells with walls very thin, trigones minute to small and concave sided, median leaf cells nearly isodiametric, variable: (24)28–42 μm wide × 28–54 μm long, the basal cells similar in size or slightly larger (to 58 μm wide and 54 μm long). Oil-bodies small for cell size, hyaline, 2–4 to 5–8(12) per cell, the surface mostly ill-defined, coarsely papillose to finely botryoidal, occasional populations coarsely botryoidal, for the most part fusiform, less often elliptic to sublinear or subglobose to globose, sometimes with 1–2 elongate concavities, 7.2–10.4 × 3.3–3.9 μm to wider and 7.2–10.4 μm × 5.2–6.5 μm to 10.4–11.7 μm × 5.2–7.2 μm, subglobose ones 7.2 × 5.9–6.5 μm, globose ones 5.2–6.5 μm in diam. Chloroplasts 3.3 × 1.3–2 μm. Underleaves much smaller than leaves, 1.6–2.7× stem width, free and in close proximity to side nearest adjacent ventral base of leaf, in some populations occasionally very narrowly connate by fusion of basalmost cells of underleaf and adjacent leaf, the insertion symmetric, inverted U-shaped, the underleaves parallel with stem to slightly spreading, contiguous to imbricate by lobe tips overlying underleaf base immediately above, plane to slightly concave (ventral view), obtrapezoid to occasionally subrectangular, bifid nearly to base and delimiting a lamina of a few cells high, the lamina rarely 5–7 cells high, the sinus often V-shaped; lobes diverging to occasionally parallel, 5–11 cells wide at base, distinctly caudate, gradually tapering to a piliform tip normally consisting of a uniseriate row of (4)5–10 cells that are moderately to distinctly longer than wide, variable, being mostly 16–26 μm wide × 34–82 μm long or 1.4–3.9× longer than wide, the lobe margins often slightly reflexed, entire or frequently with a few, often opposing ciliiform projections; underleaf base with margins plane to slightly reflexed, with a single process variable in stature and position: lobe-like to more often laciniiform to ciliiform, always smaller than the main pair of lobes, 2–6 cells wide at base, the processes positioned at the outer base of each lobe or basal to them and then on the lamina, the lamina margins sporadically armed with a few accessory cilia.

Asexual reproduction absent.

Plants autoecious, nearly always fertile. Androecia nearly always on lateral-intercalary branches, the branches either rather short, appearing to cease growth, and ca. 2× or less the length of a main shoot leaf or, more often, proliferate vegetatively distally, the androecia then basal on a branch, the branch usually less than ca. 2× the length of a main shoot leaf and only sporadically elongate; lateral-intercalary branches variable in position, at times in lateral half of underleaf axil; androecia occasionally on main shoot, only rarely on *Frullania*-type branches and then elongate and at least 3× the leaf length; androecia subfolious to subspicate; bracts much smaller than leaves if androecia on leading shoots, but if androecia on short branches, then leaves only slightly larger, the bracts suberect to spreading, dorsally assurgent throughout or dorsally assurgent and inflated in basal half, the distal half obliquely assurgent or more or less reflexed, loosely appressed to bract immediately above, the saccate portion faintly crenulate or smooth in profile and weakly fused toward base with opposite bract, the apex similar to leaves except the lobes often acuminate to subcaudate, the distal sector often less protracted; ventral margin sharply reflexed, entire or with a cilium; lobule margin involute, armed with an ill-defined, low and rounded to tooth-like or distinct and ciliiform to laciniiform distal projection, the margin otherwise with several cilia each consisting of a uniseriate filament of cells terminating in a slime papilla, the margin otherwise entire and devoid of slime papilla or crenate-dentate by protruding cells that are partially or wholly free from laterally adjoining cells, the projections each terminating in a slime papilla, the sinus between distal process and dorsal margin of lobe sometimes with a projection; antheridia solitary, the stalk uniseriate. Gynoecia mostly on main shoot or lateral-intercalary branches lacking normal vegetative leaves, rarely on elongate lateral-intercalary branches possessing many cycles of vegetative leaves; gynoecia occasionally on *Frullania*-type branches and then nearly always with several cycles of normal vegetative leaves (rarely on terminal branches lacking vegetative leaves). Bracts of innermost series much larger than leaves (especially in length), erect and ensheathing perianth, free from one another, distinctly convex to ± canaliculate distally, ovate; apex bifid to 0.35, the lobes ventrally sulcate, similar in size, caudate distally, the margins entire or with a cilium; lamina margins strongly reflexed, plane or undulate, the dorsal entire or with a cilium, the ventral with a few teeth or cilia. Bracteoles of innermost series similar to bracts in size or somewhat smaller, mostly free, sporadically narrowly connate on 1 side, distinctly concave (ventral view) to canaliculate distally, oblong to obovate but with sides straight or only slightly curved; apex bifid to 0.45, the lobes similar to those of bracts, often with a cilium on outer margin; lamina margins sharply reflexed as in bracts, entire or with a cilium or lacinium distally and a few small cilia below. Perianth exserted beyond bracts but not markedly so, sharply trigonous and prismatic throughout, the sides sometimes infolded, the perianths long and narrowly oblong, 4–4.8× longer than broad; perianth not to slightly narrowing toward the deeply 3-lobed mouth, the lobes free for ca. 0.3–0.35 the perianth length; lobes conspicuously and gradually narrowing toward apex, conspicuously bifid, the segments acuminate to (more often) subcaudate to caudate, entire or with 1–2 spinose teeth or cilia, the lobes otherwise dentate-ciliate in basal half; keels sharp, with keelar wings common, of a few to several cells high, often sparingly dentate-ciliate.

Seta 6–7 cells in diam., with 21–22 rows of outer cells surrounding a layer of cells of similar size or slightly larger, the innermost core of cells scattered and much larger, the core cells (particularly the outermost layers) with corners thickened as in knot-like trigones. Capsule wide ovate to elliptic, 41–46 μm thick, of 4 layers, the outer layer of cells equal to thickness of 1.5–2.4 of interior strata; outer layer of cells subquadrate to short rectangular, even at valve base, the radial walls rather thick, with red-brown nodular to weakly spine-like thickenings, the thickenings mostly on longitudinal walls and sporadically on transverse walls; intermediate and inner layer of cells subequal in thickness; innermost layer of cells long rectangular, the vertical radial walls sometimes with local continuous sheets or red-brown wall material that connects the bases of bands or sheets, the walls rather thick, with semiannular bands red brown, somewhat common but not copious, often incomplete, the radial walls with nodular and especially spine-like thickenings often present on longitudinal walls.

Spores 12.4–13.5 μm, red brown, with dense, low but sharply defined, close papillae and short, simple or sometimes

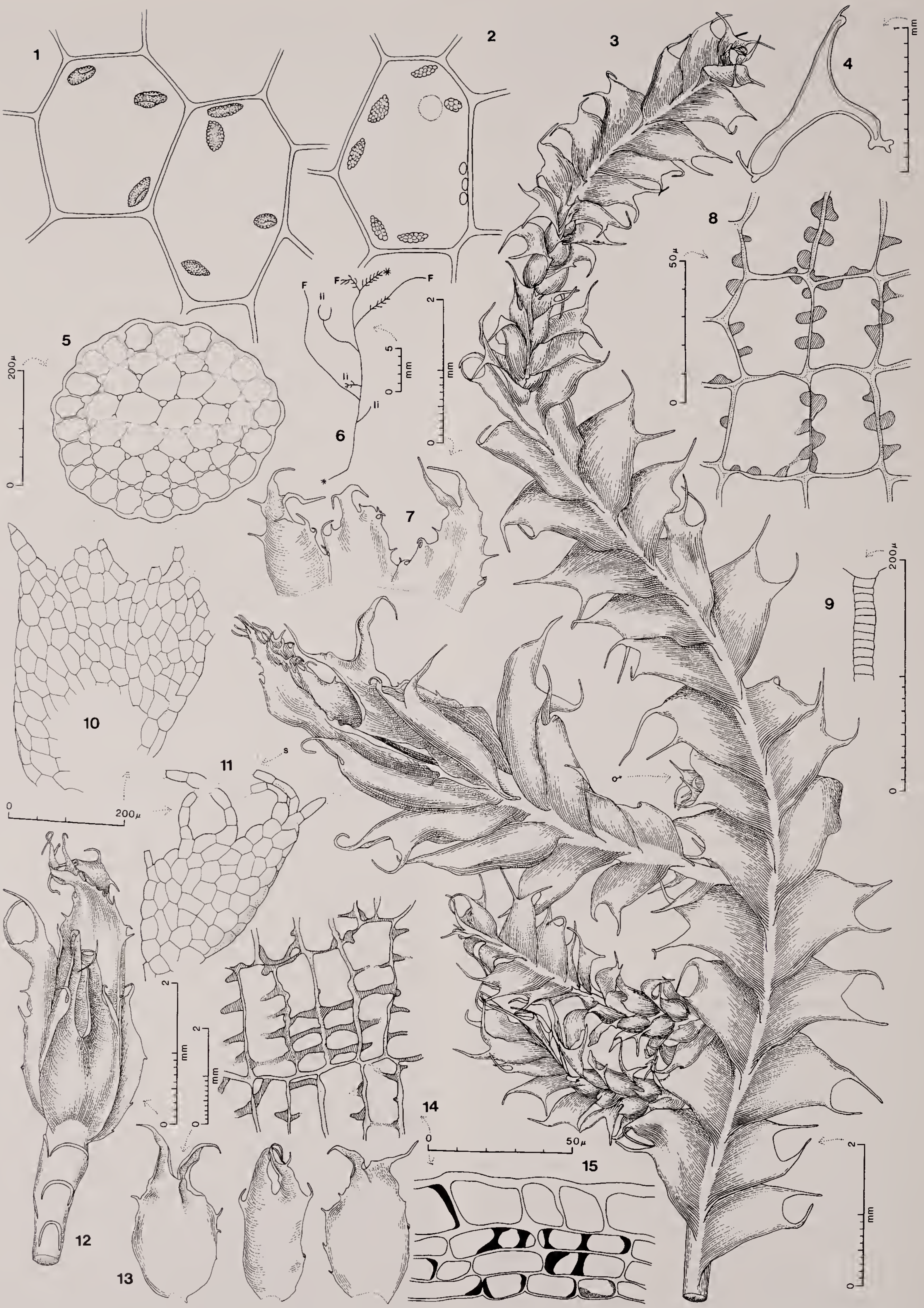


FIG. 17. *Chiloscyphus cuspidatus* (Nees) J. J. Engel & R. M. Schust. **1, 2.** Median cells with oil-bodies (636×, 654×, respectively). **3.** Sector of plant with a gynoecium on a lateral-intercalary branch and androecia on main shoot and on 3 lateral-intercalary branches, the distalmost ♂ branch consisting of only a few bracts and barely exceeding vegetative leaf (dorsal view). **4.** Perianth, cross section; note that all 3 keels are winged. **5.** Seta, cross section. **6.** Cladograph (F = *Frullania*-type branch; LI = lateral-intercalary branch; U-shaped symbol = gynoecium; * = apex and base of main shoot). **7.** Perianth mouth, ventral lobe in middle. **8.** Capsule wall, outer layer. **9.** Antheridial stalk. **10, 11.** ♂ Bract lobules; note differences in marginal armature (s [**11**] = cilium in sinus between distalmost process and dorsal margin of lobe). **12.** Gynoecium with only innermost bracts and bracteole shown, those below indicated with scars (ventral view). **13.** ♀ Bracts and in middle bracteole (note the

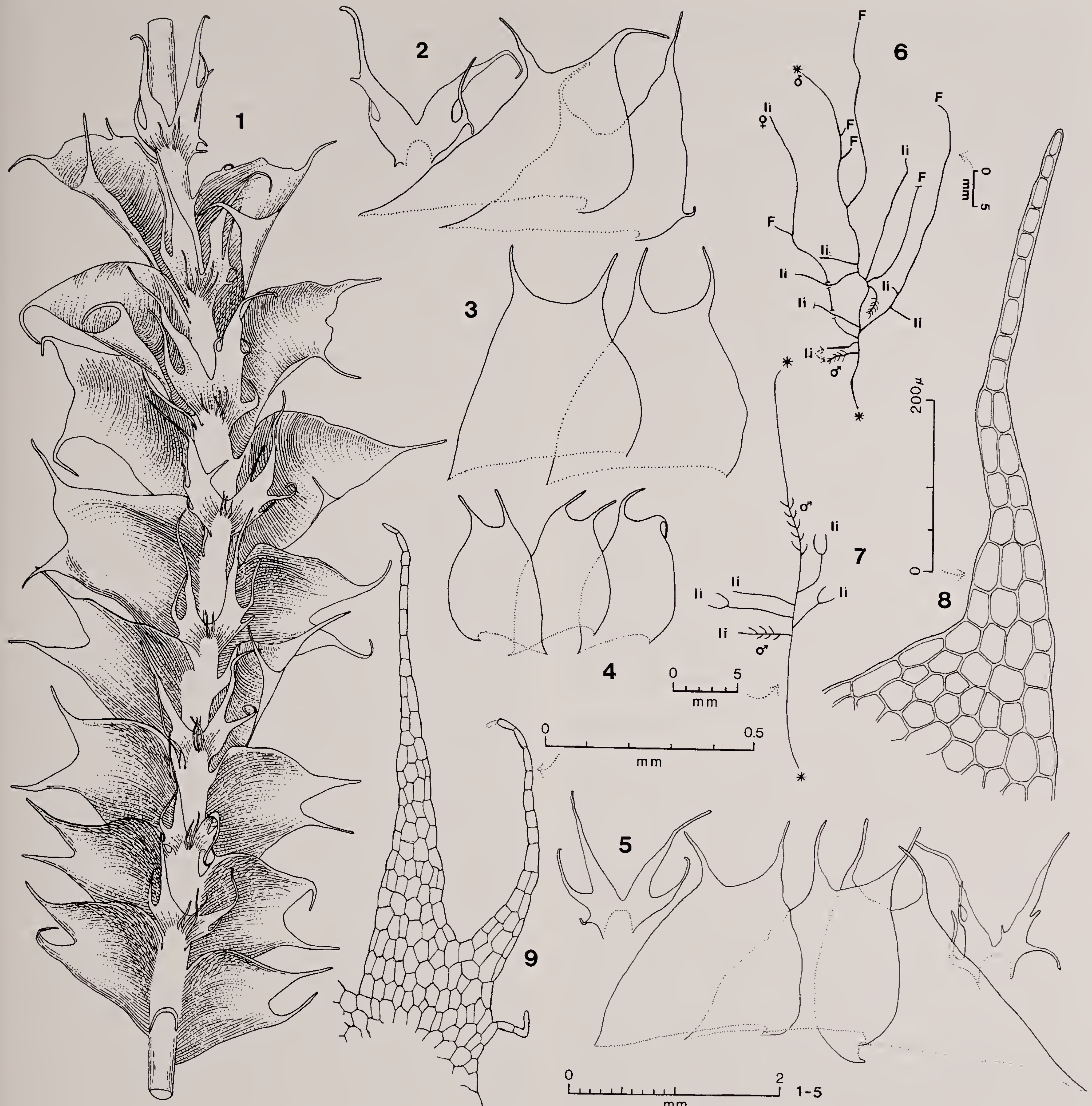


FIG. 18. *Chiloscyphus cuspidatus* (Nees) J. J. Engel & R. M. Schust. **1.** Sector of main shoot (ventral view). **2–5.** Leaves and (in **2** and **5**) underleaves. **6, 7.** Cladographs (F = *Frullania*-type branch; LI = lateral-intercalary branch; U-shaped symbol [7] = gynoecium; * = apex and base of main shoot). **8.** Portion of ventral segment of leaf. **9.** Lateral half of underleaf. (**1, 2, 5, 7–9,** from *Schuster 67-491a*, New Zealand, South Is., Mt. Cook, Natl. Park, Sealy Range; **3,** from *Engel 20196*, Tasmania, Mt. Wellington, off Pipeline Track; **4,** from *Schuster 67-4413*, New Zealand, South Is., Mt. Cook, Natl. Park, Sealy Lakes; **6,** from *Engel 13023*, Tasmania, Mt. Wellington, Fern Glade Track.)

←

magnification here is 28% less than that for leaves in Fig. 18: 2–5). **14.** Capsule wall, inner layer. **15.** Capsule wall, cross section. (**1,** from *Engel 20196*, Tasmania, Mt. Wellington, off Pipeline Track; **2,** from *Engel 20114*, Tasmania, Mt. Roland; **3, 4, 6, 7, 9, 11–13,** from *Schuster 67-491a*, New Zealand, South Is., Mt. Cook, Natl. Park, Sealy Range; **5,** from *Allison 3604*, New Zealand, North Is., E of Taupo; **8, 14, 15,** from *Engel 12996*, Tasmania, Lyell Highway near turnoff to Tarraleah; **10,** from *Engel 13023*, Tasmania, Mt. Wellington, Fern Glade Track.)

furcate, vermiculate markings, the spore:elater diameter ratio 1.4–1.8:1. Elaters tortuous, 7.2–8.6 μm wide, the spirals 2.4–2.9 μm wide.

DIFFERENTIATION—At first glance this species might be mistaken for a vigorous *C. lentus*, a species that also has distinctly bifid leaves, with lobes composed of a conspicuous uniseriate row of cells, and deeply bifid underleaves with a conspicuous lateral process on each side of the lamina. *Chiloscyphus cuspidatus* differs from that species in the 1) free underleaves; 2) larger plant size, even when suboptimal; 3) larger cell size; and 4) monoecious condition. It should be added that sex organs in *C. cuspidatus* are of much greater frequency than in *C. lentus*. *Chiloscyphus cuspidatus* is separable from all other members of sect. *Lophocolea*, except *C. longiciliatus*, by the ability to produce armature on the ventral margin of the leaf (careful search of several shoots is often required to find cilia, and often only 1 or 2 leaves of a shoot will have them), as well as by characters 2, 3 (nonenlarged cells must be used for measurement, e.g., see *C. subporosus*), and 4 above.

The closest relative of this species is *C. longiciliatus*; see under that species for a discussion.

VARIATION—The leaves are mostly loosely imbricate and broadly, evenly, and moderately convex, the whole lending a flat aspect to the shoots in dorsal view. However, occasional populations have leaves densely imbricate, and this is coupled with greater leaf convexity, both features lending the shoots a convex aspect in dorsal view. The latter condition tends to occur in smaller shoots. It also is the normal condition in well-developed plants of *C. longiciliatus*, which, when optimal, are vigorous, being 3.2–3.6 mm wide.

The student should be aware of the range of leaf shape variability when working with this species. Robust phases are asymmetrically ovate-trapezoid to trapezoid and up to 1.3× wider than long (Fig. 18: 2; *Schuster 67-491a*). However, some populations of the robust phase have subsymmetric leaves up to 1.2× longer than wide (Fig. 18: 3; *Engel 20196*). Populations with a greater length/width ratio tend to occur in smaller, but not necessarily weak, phases. For example, *Schuster 67-4413* has subsymmetric, rather narrowly ovate leaves that are 1.3–1.6× longer than wide (Fig. 18: 4). Leaf symmetry is correlated with the degree of curvature of the dorsal margin and extent of dilation of the ventral, primarily basal, sector of the leaf.

Coupled with plasticity of vegetative characters is variability of male bract lobules. The two extremes appear quite different. On the one hand, androecia, such as in *Schuster 67-491a*, have lobule margins with a distal prominent ciliiform to laciniiform process and several cilia below, each of which terminates in a slime papilla. Such lobules otherwise lack crenulations, teeth, or slime papillae (Fig. 17: 11). Lobules of the other extreme (as in *Engel 13023*) often have an ill-defined distal process, but the margin below differs in being crenate-dentate and having several slime papillae; one or a few short cilia also may be present (Fig. 17: 10). Such lobules also occur throughout *C. longiciliatus*.

Oil-body number in *C. cuspidatus* may be inversely proportional to cell size. *Engel 20196* has median leaf cells at the larger end of the range for the species, the cells 32–40 μm wide × 37–48 μm long but only 2–4 oil-bodies per cell (Fig. 17: 1). Conversely, *Engel 20114* has median leaf cells at the smaller end of the range, with cells 25–31 μm wide × 28–40 μm long but (4)5–7 oil-bodies per cell (Fig. 17: 2). The oil-bodies of the two populations are similar in size but differ somewhat in surface characters—*Engel 20196* is coarsely papillose and often has 1 or 2 elongate concavities (Fig. 17: 1), whereas *Engel 20114* is finely botryoidal and lacks cavities (Fig. 17: 2). *Engel 18176* agrees with *Engel 20196* in having large median leaf cells (38–50 μm wide × 44–56 μm long) and papillose oil-bodies, but it differs in having a direct correlation between cell size and oil-body number, here (4)5–6(8) per cell. A direct correlation between oil-body number and cell size also exists in *Engel 18867*, which has cells 35–47 μm wide × 47–54 μm long and (3)4–7(8) oil-bodies per cell. However, oil-bodies of *Engel 18867* differ from all other observed populations of *C. cuspidatus* in being very coarsely botryoidal. Also, oil-body size is at the upper end of the range for the species, being 10.4–11.7 × 5.2–7.2 μm.

NOTE—Hodgson (1953, p. 354) and Allison and Child (1975) treated this species as *Lophocolea bidentata*, stating that it is monoecious and cosmopolitan. Most CHR specimens named *L. bidentata* are actually *C. cuspidatus*.

NOTES ON TYPE SPECIMENS—1) *Lophocolea fusca* Steph. The specimen represents a rather well-developed phase of *C. cuspidatus*. Stephani states that the plants are monoecious, and I was able to verify that condition. Gynoecia and androecia may be found on the main shoot or on short, abbreviated lateral-intercalary branches lacking normal vegetative leaves. Dehisced capsules are present, although the protologue does not mention them. Trigones are minute and not "magnis" as stated in the protologue.

2) *Lophocolea mooreana* Steph. The protologue states for locality and collector "Tasmania (Moore)." A specimen from G labeled TYPE (leg. Moore, Macquarie Harbour, Moore's Track, G 17652; duplicate in M) contains an admixture of the following species: *Chiloscyphus leucophyllus*, *Saccogynidium decurvum*, *Bazzania* sp., *Heteroscyphus* cf. *coalitus* (p. p. min.) and *Telaranea* sp. However, no element in the packet matches the protologue. The only plant with bifid leaves is *C. leucophyllus*, but that plant disagrees with the protologue in having knot-like trigones. Furthermore, perianths are described as "magna," but I found no gynoecia within the packet. (The plants of *C. leucophyllus* consist of both sterile and androecial shoots.) The protologue unfortunately lacks a description of underleaves.

Another Moore collection at G (Jones Track) consists of two corticolous, bifid-leaved elements. The first is a fragment of a plant that contradicts the protologue in being sterile and having large trigones. That element is *C. rupicola*. The other element consists of plants that rather closely agree with the protologue. However, the specimen, which has numerous perianths, disagrees with the protologue in being monoecious. I conclude that Stephani overlooked the presence of androecia, thereby mistakenly stating the plant is dioecious. Sporophytes are present, which also were overlooked by Stephani. Given the otherwise good correlation with the protologue, I have selected the Moore plant from Jones Track as lectotype. The specimen represents a well-developed, somewhat flaccid phase of *C. cuspidatus*.

The Stephani Icon (*Lophocolea* no. 156) must be ignored for purposes of typification, because it is based on an Oldfield specimen (which I could not locate after a search at G).

3) *Lophocolea cuspidata* subsp. *antipodea* R. M. Schust. Schuster (1980) distinguished this subspecies from subsp. *cuspidata* by a number of characters. Subspecies *antipodea* is described as having smaller cells, a greater number of oil-bodies per cell, and dorsal margins of leaves nearly straight. I

found a continuum, involving all of these character states, that includes both subspecies. I regard the other characters used to differentiate subspecies *antipodea* as tendencies, i.e., compared with subsp. *cuspidata* the leaf lobes tend to be more attenuated, the dorsal margin often long decurrent, and the bracts and bracteoles more strongly reflexed and with bract margins having a few more cilia. I do not believe that these differences warrant taxonomic recognition.

Distribution—Subcosmopolitan; holarctic (where temperate in distribution); upper elevations in tropical sectors of world: South Africa; Campbell Is.; Auckland Is.; New Zealand (South Is., 15–1900 m; North Is., 550–1370 m); Australia: Tasmania (100–1370 m, rarely sea level), A.C.T. (1370 m), New South Wales (1400 m).

Ecology—The species has a broad altitudinal range in Australasia. In New Zealand it is rather well represented in subalpine–alpine sites, where it occurs on boggy ground (e.g., with *Sphagnum* at bog margins) or over thick, frequently wet humus or on soil. The plants often have some protection provided by scrub, ferns, *Astelia*, or grasses (e.g., between snow tussocks or under mats of dead tussock blades). For example, at both the Rainbow Skifield and Mt. Robert Skifield sites (Nelson), the species occurs in very wet niches between tussock and covered by old tussock blades. The species occasionally occurs on peaty soil of stream banks. It also is present in the upper limits of *Nothofagus menziesii* or *Podocarpus* forests, where it may be found on shaded rock walls near waterfalls or over leaf litter. At lower elevations (especially North Is.), it is rather common under manuca (*Leptospermum*). It sporadically occurs in lower elevation *Nothofagus* forests (300–440 m on South Is.), where it may be found on rotted wood on the forest floor or over leaf litter. It also may be present in forests of *Aristotelia serrata*, *Griselinia*, *Fuchsia*, and *Pittosporum eugenioides* (330 m, Morrisons Creek, Otago Prov., *Engel 17684b*).

In New Zealand, plants are able to tolerate some degree of disturbance. They occur, for example, "on mounds under Sitka Spruce" (Conical Hill State Forest, Otago Prov., leg. *Armstrong*) and "on willow log lying on swampy ground under willow grove" (Otokia, south of Dunedin, Otago Prov., leg. *Allison*).

In Tasmania the species occurs in mid-elevation forests (460–650 m) of *Eucalyptus* or *Eucalyptus–Dicksonia*, etc., or *Eucalyptus–Pomaderris–Richea* sp., where it is found on the forest floor or on old rotted wood, particularly where there is a thick humus accumulation. It rarely is corticolous (on *Eucalyptus*, *Cassinia*, and others). In subalpine sites the plant may be found over thick wet humus, particularly under thicket cover.

North American populations differ from Australasian plants in having a narrower ecological amplitude. Schuster (1980, p. 202) stated that eastern North American plants are "apparently confined to nonorganic substrates, [and are] almost invariably found on damp to moist rocks associated with running water."

Specimens Seen (selected)—**CAMPBELL IS.:** *Poppleton s.n.* as *L. bidentata*–c. sporo. (CHR); rear of Hostel, *Poppleton 4M* as *L. biciliata* (CHR). **AUCKLAND IS.:** *Hooker s.n.* as *L. multipenna* (CHR). **NEW ZEALAND. STEWART ISLAND:** Track to Mason's Bay, ca. 1–1.8 km W of Freshwater Hut/Landing, 5 m, *Engel, von Konrat & Braggins 24439* (F). **SOUTH ISLAND. SOUTHLAND:** Garvie Range, East Dome, ca. 1370 m, *Child H 3906* (F); Fiordland Natl. Park, summit of Borland Saddle, off track to Mt. Burns, S of South Branch of Borland Burn, W of Monowai, 1090 m, *Engel 18653* (F); ibid., off track along East Branch of Eglinton River, SE of Mt. Eglinton and NNE of Te Anau, 440 m, *Engel 18755*–c. ♂ (F); ibid., Gertrude Valley, off track to Gertrude Saddle, NE of Homer Tunnel, 1880–1900 m, *Engel 18867* (F). **OTAGO:** Catlins River area, *Child H 1628* as *L. bidentata*–c. ♂ (F); ibid., Ajax Swamp, ca. 1 km N of Ajax Hill, ca. 550–610 m, *Child H 5507*, *H 5550* (F); Conical Hill State Forest, (S of) Tapanui, *Armstrong s.n.* as *L. bispinosa* (CHR); Otokia, S of Dunedin, ca. 15 m, *Allison H 1349*, *H 1371*, both as *L. bidentata* (CHR); Waipori Gorge, S of Dunedin, *Allison H 1364* as *L. bidentata* (CHR); Mt. Maungatua, W of Mosgiel, summit plateau, 825 m, *Engel 17735*, *17742*, *17764A* (F); Dunedin, Abbott's Hill, *Simpson s.n.*–c. sporo. (CHR); near Lee Stream, Hindon Road, ca. 305 m, *Child H 894* as *L. bidentata* (F); Flagstaff, NW of Dunedin, ca. 455 m, *Child H 1067* as *L. subporosa*–c. sporo. (F); Mt. Cargill, N of Dunedin, ca. 455 m, *Child H 775* as *L. bispinosa* (F); ibid., ibid., W of summit road, ca. 455 m, *Child H 1711* (F); Morrisons Creek, N of Dunedin, 330 m, *Engel 17684b*–c. per. + ♂ (F); Rock and Pillar (Range), ca. 1065 m, *Child H 4986* (F); near Herbert, ca. 185 m, *Allison H 1376* as *L. bidentata* (CHR); Kakanui Range, Mt. Pisgah, ca. 915 m, *Child H s.n.114* as *L. lenta* (F); Paradise, Jordan River, head of Lake Wakatipu, ca. 365 m, *Child H 2409* as *L. bispinosa* (F); ibid., Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, *Child H 124* as *L. bidentata* (F); Fiordland Natl. Park, Martin's Bay, N of McKerrow River, *Hatcher 1062* (F); Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, 1370–1470 m, *Engel 17900B* (F); same loc., ca. 1370 m, *Child H 4170* (F). **WESTLAND:** Jackson, *Goebel s.n.* as *L. lenta*–c. sporo. (M); Westland Natl. Park, track to Alex Knob, off track to Louisa Peak, 1170 m, *Engel 18971* (F). **CANTERBURY:** Mt. Cook Natl. Park, Sealy Range, around Sealy Lakes, *Schuster 67-4411*, *67-4413* (F); ibid., E facing slope of Mt. Wakefield, just below Wakefield Falls, 870 m, *Engel 18176* (F). **NELSON:** St. Arnaud Range, Rainbow Skifield, S of St. Arnaud, 1360–1480 m, *Engel 22778*–c. per. + ♂ (F); Nelson Lakes Natl. Park, E slope of Robert Ridge in vicinity of Mt. Robert Skifield, W end of Lake Rotoiti, 1400–1480 m, *Engel 22833*–c. per. + ♂ (F); Mt. Arthur, 1350–1525 m, *Brown 88/29*, *88/52b* as *L. bidentata* (AK). **NORTH ISLAND. WELLINGTON:** W Ruahine Mtns., Whanahuia Range, 1–1.5 mi. W of Mt. Mangahuia, ca. 1370 m, *Schuster 67-571* (F); near Pukekaikiore, W of Mt. Ngauruhue, *Braggins s.n.* (AK); near eastern border of Tongariro Natl. Park along road to Tree Trunk Gorge, ca. 0.5 km W from gorge, 750 m, *Engel 21220*–c. per. + ♂ (F). **HAWKE'S BAY:** Wairoa, "Kiwi," *Hodgson 43* as *L. bidentata*–c. sporo. (CHR); ibid., Te Tiki, *Hodgson 615* as *L. bidentata*–c. sporo., *2904* as *L. bidentata*–c. sporo. (CHR). **SOUTH AUCKLAND:** E of Taupo, ca. 610 m, *Child H 1416* as *L. bidentata* (F); ibid., ca. 610–670 m, *Allison H 3604* as *L. bidentata*–c. sporo., *H 3605* as *L. bidentata* (CHR); Kaingaroa Plains, Rotorua region, *Allison H 3415*, *H 3599*, both as *L. bidentata* (CHR); ibid., ibid., "Mile Plantation," *Allison H 3600* as *L. bidentata* (CHR); E of Waiotapu Valley, Rotorua region, ca. 550 m, *Allison H 3601*, *H 3603*, both as *L. bidentata* (CHR); Reporoa, S of Rotorua, *Allison H 3602* as *L. bidentata* (CHR); near Atiamuri, S of Rotorua, *Allison H 3658*, *H 3659*, *H 3661*, *H 3662*, *H 3663*–c. sporo., *H 3715*, all as *L. bidentata* (CHR); between coast and Lake Rotorua, Bay of Plenty, *Allison H 3430* as *L. bidentata*–c. sporo. (CHR). **TASMANIA.** Blue Tier, *Rodway s.n.* as *L. bidentata* (HO); Ringarooma, *Rodway s.n.* as *L. bispinosa* (HO); near Coal Bluff, sea level–50 m, *Norris 30230* (F); Adamsons Track, *Ratkowsky s.n.* as *L. bidentata* (F); Hartz Mtn. Natl. Park, ca. 800 m, *Ratkowsky 77/162* (HO); ibid., Devils Backbone, above Lake Perry and Lake Osborne, 960–1020 m, *12829*–c. sporo. + ♂ (F); Mt. Wellington, 760 m, *Rodway s.n.* as *L. bidentata* (HO); ibid., Pipeline Track, *Ratkowsky s.n.* as *L. lenta* (F); ibid., off Pipeline Track, SE of St. Crispins Well, 640–650 m, *Engel 20196* (F); ibid., above Disappearing Tarn, *Ratkowsky 79/86* as *L. bidentata* (HO); ibid., above Silver Falls, *Ratkowsky 79/87* as *L. bidentata* (HO); ibid., along McRobies Gully, ca. 100–300 m, *Norris 29279* (F); ibid., Fern Glade, *Ratkowsky 78/144* (HO); ibid., Fern Glade Track, ca. 460–520 m, *Engel 13023* (F); ibid., Zig Zag Track, *Ratkowsky 79/88* as *L. bidentata* (HO); ibid., Thark Ridge, *Ratkowsky 80/65* as *L. bidentata* (HO); Trestle Mtn., *Ratkowsky s.n.* as *L. bidentata* (HO); Fire Roads, Knocklofty, *Ratkowsky s.n.* as *L. subporosa* (F); Mt. Field Natl. Park, N side of Lake Fenton, ca. 900 m, *Norris 28549* (F); ibid., Mt. Field, 915 m, *Rodway s.n.* as *L. bispinosa* (HO); off Lyell Hwy., near turnoff to Tarraleah, *Engel 12996*–c. sporo. + ♂ (F); Cradle Mtn.–Lake St. Clair Natl. Park, Lake St. Clair area, plateau ENE of Mt. Rufus summit, ca. 1360–1370 m, *Engel 19391*–c. ♂ (F); S end of Great Lake, at intersection of road to Bronte Park, ca. 1100 m, *Norris 33037* (F); Zion Hill, Walls of Jerusalem, *Ratkowky s.n.*

TABLE 7. Comparison between suboptimal and optimal *C. longiciliatus* and *C. cuspidatus*.

Character	*C. longiciliatus* optimal	*C. longiciliatus* suboptimal	*C. cuspidatus*
Underleaf lamina height: no. of cells high	9–15(17)	5–14	usually a few cells high
Underleaf lobing	4-lobed	2–4-lobed (even on 1 shoot); predominantly bilobed on distinctly weaker, narrower shoots	uniformly bilobed
Underleaf imbrication; stem tissue exposed in ventral view	closely imbricate; little or none exposed	contiguous to loosely imbricate; large, distinct sectors exposed	contiguous to imbricate by lobe tips overlying underleaf base immediately above; large sectors exposed
Underleaf lateral lobes: no. of cells wide	8–15	4–9(11)	2–6
Armature of underleaf lobe	consistently with 1(2) opposing processes	variable frequency of 1 pair of opposing processes: occasional to frequent, but not consistently present; some populations often entire or 1-ciliate	often with opposing ciliiform projections or entire
Stem tissue exposed in dorsal view	little or none	distinct V-shaped sectors between each leaf pair	distinct V-shaped sectors between each leaf pair
Shoot width (mm)	3.2–3.8	2.5–3	2.6–4
Examples	*Engel 19820*	*Engel 19390, 19413A*	—

as *L. bidentata* (F); summit area of Mt. Roland, just E of Gowrie Park, 1160–1200 m, *Engel 20114*–c. ♂ (F). **AUSTRALIA. A.C.T.:** Smokers Flat, 32 km SW of Canberra, 1370 m, *Streimann 1756, 1761*, both as *L. bidentata, 1765, 1769* (CBG). **NEW SOUTH WALES:** Tinderry Range, southern tablelands, S foothills near road, ca. 8 km ESE of Michelago, ca. 1400 m, *Verdon 1867* (CBG).

Chiloscyphus longiciliatus (Herzog) J. J. Engel & R. M. Schust.

> *Lophocolea longiciliata* Herzog, Memoranda Soc. Fauna Fl. Fenn. 27: 96. *f. 42.* 1952. *Chiloscyphus longiciliatus* (Herzog) J. J. Engel & R. M. Schust. Nova Hedwigia 39: 418. 1985 (1984). Holotype: Tasmania, Wilmot, 1927, *Weindorfer 35* (JE!); isotypes: (JE!, M!).

Plants rather flexuous, loosely creeping, very pale green; shoots ± convex in dorsal view, when well developed 3.2–3.8 mm wide, smaller phases 2.5–3 mm wide. Branches frequent, in some populations predominantly of lateral-intercalary type, with *Frullania*-type branches sporadic, in other populations the reverse; ventral-intercalary branches rare (1 seen); half-leaf of *Frullania*-type branch undivided and with the apex similar to a leaf lobe, or if divided (rare), then the ventral lobe much larger and the dorsal lobe appearing as a process on the dorsal margin. Rhizoids sparse, from stem at immediate base of underleaves, the rhizoids short for plant size. Leaves subopposite because of close imbrication, widely spreading, loosely to densely imbricate, free dorsally, the orientation strongly succubous, the insertion distinctly recurved at ventral end (distinctly J-shaped), the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves broadly and distinctly convex, a- to subsymmetically ovate-trapezoid to trapezoid, clearly widest near base, apex bifid to (0.2)0.25–0.35, the lobes ± parallel to diverging, plane, (the ventral often considerably larger), subcaudate, tapering from a narrowly to broadly acute basal sector to a zone of up to 5(7) tiers of 2 laterally juxtaposed cells and terminating in a piliform tip consisting of a uniseriate row of (4)5–11 cells that are variable but usually longer than wide, being 18–24 µm wide × 26–37 µm long or 1.2–2(2.6)× longer than wide and only sporadically isodiametric, the lobe margins entire, the sinus broadly rounded to lunate, occasionally with a cilium or spinose tooth; dorsal margin broadly and evenly slightly arched to straight to curved inward and lunate, plane to deflexed and, if abruptly and strongly so, then forming a weak cnemis, the margin with 1(3) processes or entire, often rather long decurrent; ventral margin broadly arched (sharply so at base), distinctly more arched than the dorsal, plane to sharply deflexed in basal sector, 1–4(5)-dentate-laciniate, at most rarely or sporadically entire. Leaf cells with walls very thin, trigones minute to small and concave sided, median leaf cells 23–36(38) µm wide × (25)28–38(41) µm long, the basal cells similar in size or slightly larger, 34–42 µm wide × 35–46(49) µm long. Oil-bodies in all cells except distalmost cell of uniseriate row of leaf segments, occupying small fraction of cell volume, hyaline and glistening, 2–4 to (3)4–6(10) per cell, subglobose grading to fusiform (sometimes ± asymmetrically so), some 13–13.7 × 5.2–6.5 µm, some 7.8–9.8 × 3.3–4.6 µm, others globose and 4.6–6.5 µm in diam., coarsely botryoidal, the segmentation distinct, the spherules very large, 2–2.6 µm in diam., many oil-bodies only 3–4 spherules wide. Underleaves similar to leaves in size or moderately smaller, 1.9–3.4(3.9)× stem width, free but in close proximity to side nearest adjacent ventral base of leaf, in rare populations occasionally very narrowly connate by fusion of basalmost cells of underleaf and adjacent leaf, the insertion symmetric, inverted U-shaped, the underleaves slightly to moderately spreading, in well-developed shoots closely imbricate and covering stem or nearly so in ventral view, in suboptimal plants contiguous to loosely imbricate by lobe tips overlying underleaf immediately above, but in either case distinct sectors of stem are exposed, the underleaves varying from slightly concave to plane to slightly convex (ventral view), obtrapezoid to subquadrate to subrectangular, 4-lobed (well-developed shoots) to 2–4 to occasionally 2-lobed (suboptimal shoots), the median sinus descending to (0.5)0.55–0.75, the lateral pair of sinuses of equal depth or the median sinus slightly shallower, the lamina distinct, variable in height, often distinct and then 5–17 cells high, less often reduced and less than 4 cells high, the sinus often V-shaped; median lobes diverging to occasionally parallel, 9–17(24) cells wide at base, subcaudate-caudate, gradually tapering to a piliform tip normally consisting of a uniseriate row of (4)5–10(14) cells that are moderately to distinctly longer than wide, variable, being mostly 18–28 µm wide ×

(32)37–49(52) μm long or 1.3–2.6× longer than wide, the lobe margins often slightly reflexed, with 1(2) pair of opposing ciliiform-laciniiform processes and 1–2 accessory cilia (optimal shoots), the suboptimal shoots at times with opposing armature occasional or the margins entire or 1-ciliate; lateral lobes uniformly smaller than the median, 8–15 cells wide at base on optimal shoots, 4–9(11) cells wide on suboptimal ones, the margins with 1–3 cilia, 2 of which are opposite, often entire or 1-ciliate in suboptimal plants; underleaf lamina margins plane to slightly reflexed, with a laciniiform to ciliiform process always much smaller than the main lobes, the lamina margins often armed with a few accessory cilia.

Asexual reproduction rare, by regeneration from *in situ* leaves.

Plants autoecious, nearly always fertile. Androecia occasionally on main shoot but more often on long *Frullania*-type branches or lateral-intercalary branches that vary from rather short and ca. 2× the length of a main shoot leaf to rather long; androecia subfolious to subspicate; bracts moderately to much smaller than leaves, suberect to spreading, strongly dorsally assurgent throughout, rather closely appressed to bract immediately above, the saccate portion smooth in profile and fused toward base with opposite bract, the apex similar to leaves except the lobes often acuminate to subcaudate, the distal sector often less protracted; ventral margin sharply reflexed, entire; lobule margin involute, armed with a distal ciliiform to laciniiform projection, the margin otherwise crenulate-dentate by cells that are partially or wholly free from laterally adjoining cells or laterally fused the entire length with only the free end forming a convex projection, the margin often also with a few cilia, the projections each terminating in a slime papilla, the sinus between distal process and dorsal margin of lobe sometimes armed; antheridia solitary, the stalk uniseriate. Gynoecia on main shoot or long *Frullania*-type branches or lateral-intercalary branches that are either long or, if short, either lacking normal vegetative leaves (or with only a few gyres); gynoecia rarely on ventral-intercalary branches (1 branch seen). Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free from one another, convex to ± canaliculate distally, elliptic; apex bifid to 0.25, the lobes ventrally sulcate, similar in size, subcaudate-caudate distally, the margins entire or with 1–2 cilia; lamina margins reflexed, plane or undulate, the dorsal entire or with several cilia, the ventral sparingly dentate-laciniate. Bracteoles of innermost series similar to bracts in length but somewhat narrower, free, weakly concave (ventral view), narrowly elliptic to narrowly obovate; apex bifid to 0.3, the lobes similar to those of bracts, entire or with a cilium or opposing pair of cilia; lamina margins reflexed as in bracts, with a lacinium or lobule distally and entire or sparingly ciliate below. Perianth exserted beyond bracts but not markedly so, sharply trigonous and prismatic throughout, the sides sometimes infolded, the perianths long and narrowly oblong, 3.5–4.8× longer than broad, not to slightly narrowing toward the deeply 3-lobed mouth, the lobes free for ca. 0.25–0.3 the perianth length; lobes conspicuously and gradually narrowing toward apex, conspicuously bifid, the segments subcaudate to caudate, entire or with 1–2(3) spinose teeth or cilia, the lobes otherwise dentate-ciliate in basal half; keels sharp, with keelar wings common, of a few to several cells high, often dentate-ciliate.

Sporophyte not seen.

Differentiation—This is a distinctive species, especially when well-developed plants are at hand. The closest ally is *C. cuspidatus*, and optimal plants of *C. longiciliatus* are clearly distinct from that species. However, suboptimal populations must be treated with care, in that the variation spectrum of *C. longiciliatus* extends toward *C. cuspidatus*. Therefore, it is important that the traits of suboptimal plants be noted and contrasted to the optimal phase; both are compared with *C. cuspidatus* in Table 7.

Chiloscyphus longiciliatus is distinct from *C. cuspidatus* in a number of features. *Chiloscyphus longiciliatus* has a much higher frequency of leaf armature, and processes may be present on the ventral and dorsal margins as well as the sinus base (Fig. 19: 5, 6, 12). Armature of *C. cuspidatus* is only sporadic, and then only on the ventral margin (Fig. 18: 2). Underleaves of *C. longiciliatus* are often 4-lobed and often have a lamina high for the section (Fig. 19: 8, 10), whereas those of *C. cuspidatus* are always bilobed and have a lamina, at most, a few cells high (Fig. 18: 5, 9). Oil-body differences also will distinguish the species.

Notes—1) Leaf insertions may define a long and very narrow slit of stem tissue, lending the shoots a distinctive appearance in dorsal view. Some variability may occur, even on one shoot, where the slit is parallel sided and stem tissue may be completely covered, or the slits gradually somewhat widen apically between each opposing leaf pair (i.e., the exposed stem tissue is narrowest between dorsal sectors of opposing leaves). The variation is correlated with vigor, and differences in this feature lend quite different aspects in dorsal view (compare Fig. 19: 1 with 12).

2) Several interesting "freaks" occur on long, lateral-intercalary branches of *Engel 19413A*. The two dorsal faces of the perianth are formed, but the ventral is totally lacking. Normal vegetative leaves and underleaves occur distal to the perianth lobes, and after 3–4 gyres, a young gynoecium is produced. This was also observed in *Engel 19382*.

3) *Chiloscyphus cuspidatus* has an interesting inverse correlation between oil-body number and cell size (see p. 54). This does not exist in *C. longiciliatus* because those populations that have a higher oil-body number (*Engel 19387*, *19820*, both with 4–6[10] per cell) have slightly larger median leaf cells (24–38 μm wide × 30–41 μm long). Populations with lower oil-body numbers (*Engel 19382*, with 2–4 per cell) have smaller cells (23–30 μm wide × 25–38 μm long).

Notes on Type Specimen—*Lophocolea longiciliata* Herzog. The specimen represents a vigorous expression of the species, largely agreeing with the optimal phase in Table 7. Perianths are juvenile as stated in the protologue; they do not extend beyond subtending bracts. The plant is autoecious, not dioecious as stated in protologue.

Distribution and Ecology—This infrequent Tasmanian endemic occurs in mosaics of low subalpine scrub (dominated by *Richea scoparia*, *R. sprengelioides*, *Orites revoluta*, and others) and cushion plants among boulders and rocky outcrops (1260–1370 m). It may be found terrestrially, well under dense cover of shrubs, or among grass on rill banks, as well as on slopes just above seepage areas with *Sphagnum*, *Astelia*, *Drosera*, and others. The plant also is known from higher elevation forests (920–1080 m in Weindorfers Forest).

Specimens Seen—**TASMANIA.** Cradle Mtn.–Lake St. Clair Natl. Park, Lake St. Clair area, plateau ENE of Mt. Rufus summit, 1360–1370 m, *Engel 19390*, *19413A* (F); ibid., Cradle Mtn. area, Weindorfers Forest, ca. 920–1080 m, *Jarmen 88/15*–c. sporo., *88/16*

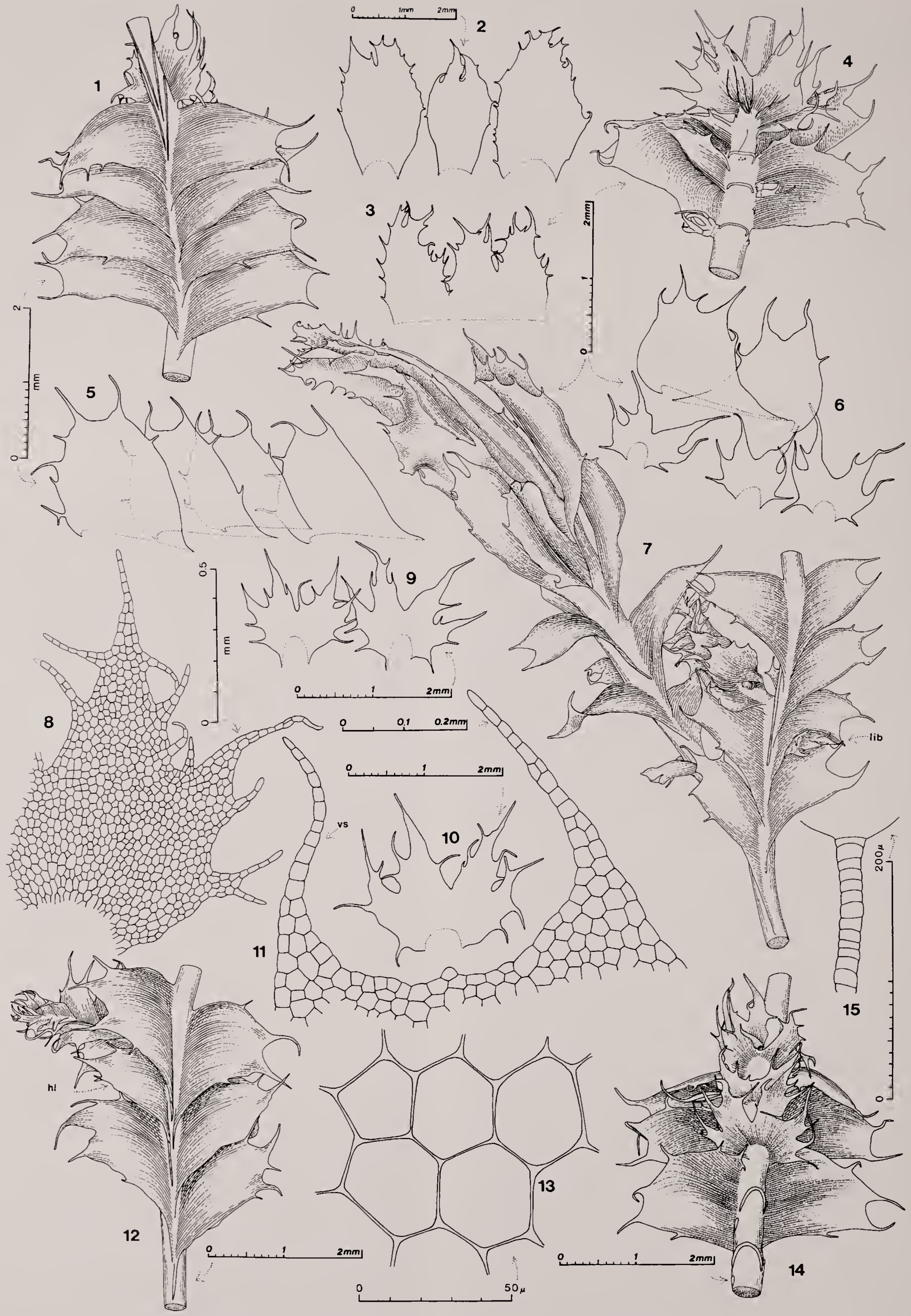


FIG. 19. *Chiloscyphus longiciliatus* (Herzog) J. J. Engel & R. M. Schust. **1.** Sector of main shoot, dorsal view. **2.** ♀ Bracts and in middle, bracteole (note figure drawn at 72% of that of leaves). **3.** Perianth mouth, ventral lobe in middle. **4.** Sector of main shoot, ventral view; note position of lateral-intercalary branches. **5, 6.** Leaves and, below **6**, underleaves. **7.** Sector of main shoot with androecium and gynoecium, each on lateral-intercalary branches, dorsal view. (Note leaf at left removed to show details of androecial branch; LIB = lateral-intercalary branch [sterile].) **8.** Lateral half of underleaf. **9, 10.** Underleaves. **11.** Leaf apex; vs = ventral segment. **12.** Sector of main shoot with *Frullania*-type branch, dorsal view; note half-leaf (= HL). **13.** Median leaf cells. **14.** Sector of main shoot, ventral view. **15.** Antheridial stalk. (**1, 4, 5, 8, 10, 11,**

(F); immediately below summit of Black Bluff, SW of Nietta, 1260–1300 m, *Engel 19820* (F).

Chiloscyphus herzogii J. J. Engel & R. M. Schust.

> *Chiloscyphus herzogii* J. J. Engel & R. M. Schust., Nova Hedwigia 39: 416. 1985 (1984), *ut nom. nov. pro Lophocolea decurrens* Herzog, Trans. & Proc. Roy. Soc. New Zealand 65: 352. 1935, *non Chiloscyphus decurrens* (Reinw., Blume & Nees) Nees *in* Gottsche, Lindenb. & Nees, Syn. Hep. 173. 1845. Holotype: New Zealand, South Is., Nelson Prov., Mt. Arthur, Tableland Track, 3 Feb. 1930, *Sainsbury 37* (JE!–c. per. + ♂); isotypes: (CHR!, JE!).

Plants with a ± spinose appearance, soft, flexuous, rather spongy, loosely creeping in rather tightly interwoven mats, pale green; shoots to 0.8 mm wide, strongly bilaterally compressed. Branches frequent, of *Frullania* and lateral-intercalary types, the terminal branching somewhat more common, the lateral-intercalary branches often short (to 1.6 mm long), spike-like and at times ± clasmatocoleoid in appearance, at other times similar in appearance to main shoots, the intercalary branches variable in position: from ventral-lateral to nearly ventral, occasionally in lateral half of underleaf axil. Stems 9–10 cells high, the cortex moderately differentiated, the lateral and dorsal cortical cells in 1–2 rows of somewhat larger cells, the ventral cortical cells much smaller and poorly differentiated, the medullary cells decreasing in size from dorsal to ventral; stem cells mostly thin walled, the ventral medullary and cortical cell walls feebly thickened. Rhizoids in dense, often rather large fascicles from stem at immediate base of underleaves, the tips often branched. Leaves alternate, maximally dorsally assurgent, the leaves vertical and squarrose dorsally or nearly so, the adaxial faces of opposing leaves aligned toward one another and often closely juxtaposed, the leaves loosely imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion of opposing leaves extending to the dorsalmost laterally juxtaposed rows of stem cells and not to exact midpoint of stem. Leaves broadly concave, strongly asymmetrically broadly deltoid, the dorsal base of leaf abruptly dilated, resulting in a conspicuous, acute flange of tissue that extends toward shoot base at least to a point that roughly intersects a vertical line from dorsal lobe of the leaf immediately below, the leaf base 1.7–2.4× the width of the leaf at its midpoint; apex bifid to (0.25)0.35–0.55, the lobes variable in orientation, sometimes connivent, sometimes diverging, plane to somewhat ventrally sulcate, subequal or, more often, the ventral slightly to markedly shorter, the lobes subcaudate-caudate, the tip terminating in a uniseriate row of (3)4–6 cells, the lobe margins entire but often ± crenulate; dorsal margin forming a broad lunate to broadly sinuate line, plane to undulate, entire but often ± crenulate; ventral margin broadly and slightly curved, plane, entire, often ± crenulate. Leaf cells with walls thin, trigones minute to small or lacking, median leaf cells 25–37 µm wide × 28–40 µm long; surface smooth. Underleaves much smaller than leaves, ca. 1.2–1.4× stem width, narrowly and inconspicuously connate on both sides, the insertion often asymmetric, crescent shaped, the underleaves slightly spreading, distant to approximate, usually plane to slightly convex (ventral view), mostly cuneate, occasionally narrowly ovate to subrectangular; apex bifid nearly to the base, the lamina of only a few cells high; lobes ± parallel to (mostly) diverging, subcaudate-caudate, the lobe margins entire; lamina margins plane, entire or with a small tooth.

Asexual reproduction absent.

Plants dioecious. Androecia on leading shoots or elongate, indeterminate *Frullania*-type branches, initially terminal but eventually become intercalary, sporadically on indeterminate lateral-intercalary branches, the ♂ branches sometimes appearing to cease growth, but at other times proliferating vegetatively distally (the androecium then basal on a lateral branch). Androecia of two types: 1) bracts nearly identical in shape, size, and orientation to vegetative leaves except for development of a small lobule, the bracts somewhat more closely imbricate than leaves; and 2) androecia on smaller, often reduced, slender shoots, the bracts strongly ventricose-cucullate, so much so that the dorsal pocket is ill-defined, the androecia then wider than sterile portions of shoot. Bracts with saccate portion smooth in profile and fused toward base with opposite bract; lobule margin inflexed, the free margin crenate-denticulate, with slime papillae, often with 1 or 2 of teeth larger; antheridia solitary, the stalk uniseriate. Gynoecia on main shoot and rather short *Frullania* and lateral-intercalary branches (with several cycles of normal leaves). Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free from one another, with a broad concavity that conforms to the contours of the perianth, narrowly ovate, distinctly narrowing toward the apex; apices bifid to ca. 0.4, the lobes acuminate to caudate, ventrally sulcate, undulate, entire; lamina margins ± evenly arched, often reflexed, often with a dentiform to laciniiform process in median or distal sector, at times also with a small tooth below, at times completely entire. Bracteoles of innermost series 0.5–0.6× area of bracts, free or very narrowly connate on 1 side, distinctly and broadly convex (ventral view), ± elliptic; apex similar to bracts; lamina margins sharply and narrowly reflexed and with a dentiform to laciniiform process in distal sector or entire. Perianth inflated-trigonous in basal half, the distal half rather sharply trigonous, the perianths subrectangular to elliptic to narrowly ovate, slightly narrowing toward the wide, deeply 3-lobed mouth, the 2 lateral lobes deeply bifid and with segments acuminate to subcaudate, ventrally sulcate, and entire, the ventral lobe less deeply divided, often short bifid and with short-acuminate segments, the 3 lobes otherwise sparingly spinose-dentate-laciniate below level of segments; keels rather sharp (especially distally), with keelar wings lacking or low and then entire or sparingly armed.

Sporophyte not seen.

Differentiation—This is a well-defined species that may be distinguished immediately from all other Australasian members of the genus by the vertical, dorsally squarrose, entire-margined leaves that have a distinctive shape—the dorsal base is conspicuously dilated, forming an acute flange of tissue that extends for a considerable distance toward the shoot base (Fig. 20: 10). The maximally dorsally assurgent leaves are a striking feature, and adaxial faces of opposing leaves are aligned toward one another (Fig. 20: 10). *Chiloscyphus herzogii* is the only member of the section with underleaf

←

13–15, from *Engel 19820*, Tasmania, Black Bluff; **2, 3, 6, 7, 12,** from *Engel 19413A*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park, Lake St. Clair area, ENE of Mt. Rufus summit; **9,** from *Engel 19390*, same loc. as *Engel 19413A*.)

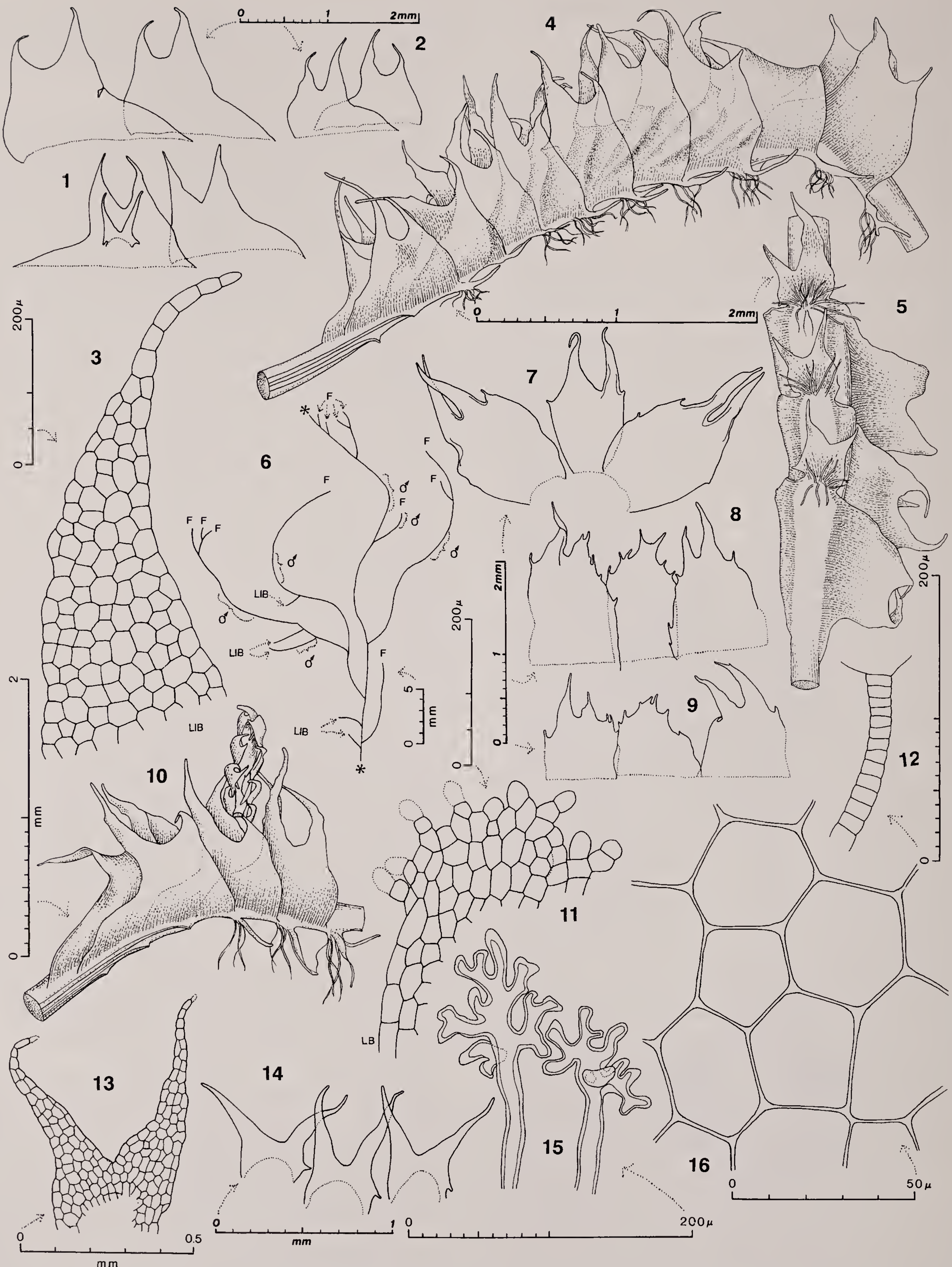


FIG. 20. *Chiloscyphus herzogii* J. J. Engel & R. M. Schust. **1.** Four leaves and, lower left, an underleaf drawn within at same scale. **2.** Two leaves. **3.** Portion of dorsal segment of leaf. **4.** Sector of leading shoot (the portion indicated by stipple in cladograph showing minimal differentiation of androecial bracts; lateral view. **5.** Sector of main shoot, ventral view. **6.** Cladograph (* = base and apex of main shoot; F = *Frullania*-type branch; LIB = lateral-intercalary branch; ♂ = androecia; stipple outline indicates sector drawn in fig. 4). **7.** Bracts and in middle, bracteole. **8, 9.** Perianth mouths, ventral lobes of each in middle. **10.** Sector of main shoot (note spike-like lateral-intercalary branch = LIB); lateral view. **11.** ♂ Bract margin (LB = lobule base). **12.** Antheridial stalk. **13.** Underleaf. **14.** Underleaves. **15.** Rhizoid tips. **16.** Median leaf cells.

connation consistently on both sides (Fig. 20: 5).[3] Distinctive also are the male bracts, which on well-developed shoots are virtually indistinguishable from vegetative leaves except for presence of a lobule (Fig. 20: 4).

Some characters, namely the deeply bifid leaves and underleaves connate on both sides, argue for placement in sect. *Spiniferi*. However, *C. spinifer*, the sole member of that section, has biseriate antheridial stalks and conspicuous, (4)6-lobed, asteroid underleaves.

Notes on Type Specimen—*Lophocolea decurrens* Herzog. The specimen is rather small and somewhat suboptimal for the species. The dilated sector is less pronounced and leaf lobes less attenuated than in optimal populations.

Distribution and Ecology—Known only from South Is., New Zealand (490–1190 m). This infrequent species occurs on rotted wood within *Nothofagus menziesii* forests; it sometimes is mixed with *C. subporosus* or *C. bispinosus*.

Specimens Seen—**NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, summit of Borland Saddle, off track to Mt. Burns, S of South Branch of Borland Burn, 1090 m, *Engel 18662*–c. per. + ♂ (F). **WESTLAND:** Mt. Brewster, NE of Haast Pass, 490–975 m, *Schuster 67-3701*–c. per. (F). **NELSON:** Nelson Lakes Natl. Park, Mole Stream, above Mole Hut, 1190 m, *Simpson 4066* as *L. subporosa*–c. per. + ♂ (CHR); Mt. Arthur, Tableland Track, *Sainsbury s.n.*–c. young per. + ♂ (CHR).

Chiloscyphus excisifolius (Steph.) J. J. Engel & R. M. Schust.

> *Lophocolea excisifolia* Steph. *in* Steph. and Watts, J. & Proc. Roy. Soc. New South Wales 48: 118. 1914. *Chiloscyphus excisifolius* (Steph.) Engel & R. M. Schust., Nova Hedwigia 39: 414. 1985 (1984). Type: Australia, New South Wales, Hot Springs, Yarrangobilly Caves, Jan. 1906, *Watts 924a* (G!–c. ♂, NSW!–c. ♂).

Plants brittle, flexuous, rather strongly dorsiventrally flattened, apparently prostrate, pale green, translucent; shoots to 3.8 mm wide. Branches sparing, mostly of lateral-intercalary type, occasionally of *Frullania* type; intercalary branch position variable: sometimes between ventral base of leaf and underleaf base or (often) from ventral-lateral side of stem between 2 underleaves. Stems 9–11 cells high, the cortex poorly differentiated laterally and dorsally, ± equal in size to medullary cells, the ventral cortical cells feebly differentiated, in 1 row of cells somewhat smaller than those of medulla; cortical and medullary cells thin walled. Rhizoids sparingly developed, from stem at immediate base of underleaf. Leaves translucent, distinctly alternate, subhorizontal, widely spreading, approximate to feebly imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending dorsally to variable degrees but never to stem midline and thus delimiting a leaf-free strip of (1)2–5 stem cells wide. Leaves plane to ± slightly convex, asymmetrically to subsymmetrically ovate (often widely so) to ovate-subtrapezoid, sometimes widest at base, at times widest at or immediately below leaf middle; apex bifid to 0.2–0.35, the lobes ± parallel to slightly diverging, plane, subequal or the ventral larger, the lobes apiculate to acuminate, tapering from a narrowly to broadly acute basal sector to a zone of up to 5 tiers of 2 laterally juxtaposed cells and ultimately terminating in a uniseriate row of 4–5 cells, the lobe margins entire, the sinus rounded, sometimes lunate; dorsal margin ± straight to broadly and slightly curved, plane, entire, decurrent; ventral margin broadly arched, often more strongly so than dorsal margin, plane, entire. Leaf cells with walls notably thin, trigones lacking; median leaf cells 29–40 µm wide × 30–42 µm long; surface smooth. Underleaves much smaller than leaves, 0.95–1.4× stem width, free, the insertion crescent shaped, the underleaves often strongly spreading to squarrose to recurved, distant, plane to concave (ventral view), subelliptic to long rectangular to cuneate, the apex bifid to 0.7–0.9, the lamina mostly of 2–5 cells high; lobes ± parallel to diverging, caudate, terminating in a uniseriate row of 4–9 cells, the lobes plane, entire; lamina margins plane to slightly recurved, with a single dentiform to ciliiform process, otherwise devoid of other armature.

Asexual reproduction lacking.

Plants apparently dioecious (gynoecia unknown). Androecia on main shoot or on elongate, indeterminate, lateral-intercalary branches, subfolious to subspicate; bracts considerably smaller than leaves, strongly dorsally assurgent, rather tightly appressed to bract immediately above, the saccate portion smooth in profile and fused toward base with opposite bract, the bracts ventricose in basal portion, the distal portion erect and stiffly vertical to distinctly reflexed and more leaf-like in orientation, the apex often similar to leaves in lobe form (but less strongly acuminate), at other times (in subspicate androecia) the lobes becoming reduced and strongly asymmetric—the dorsal lobe reduced, tooth-like, and basal in juxtaposition to the large ventral lobe, the ventral margin of bract entire; lobule margin inflexed, the distal sector with a conspicuous dentiform to laciniiform process, and basal to this process are several few-celled teeth that terminate in a slime papilla, the sinus between the dorsal margin of the lobe and the distal tooth of the lobule often with 1–3 teeth; antheridia solitary, the stalk uniseriate. ♂ Bracteoles strongly spreading.

Sporophyte not seen.

Differentiation—This species and *C. anisolobus* are unique, at least in our taxa of sect. *Lophocolea*, by possessing a dorsal leaf-free gutter (Fig. 21: 6) (for notes on differentiating the two species, see under *C. anisolobus*). The species is related to *C. subporosus*, which also has free underleaves and, usually, leptodermous cells. It differs from that species in the predominance of intercalary branching, the larger leaf cells, which are relatively uniform in size (i.e., without scattered large intramarginal cells), the smaller underleaf size (being only 0.95–1.4× the stem width), and the smaller underleaf disc armature.

←

(**1, 3–6, 8, 10–16,** from *Engel 18662*, New Zealand, South Is., Fiordland Natl. Park, summit of Borland Saddle; **2, 7, 9,** from *Schuster 67-3701*, New Zealand, South Is., Mt. Brewster.)

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[3] This feature is not easily studied because connation on both sides is narrow, and it is comparatively difficult to position the strongly laterally compressed shoots to provide a direct ventral view. I have examined leaf–underleaf connation in this species by aligning shoots to provide a dorsal-lateral view, followed by careful teasing of leaves to expose attachment with underleaves.

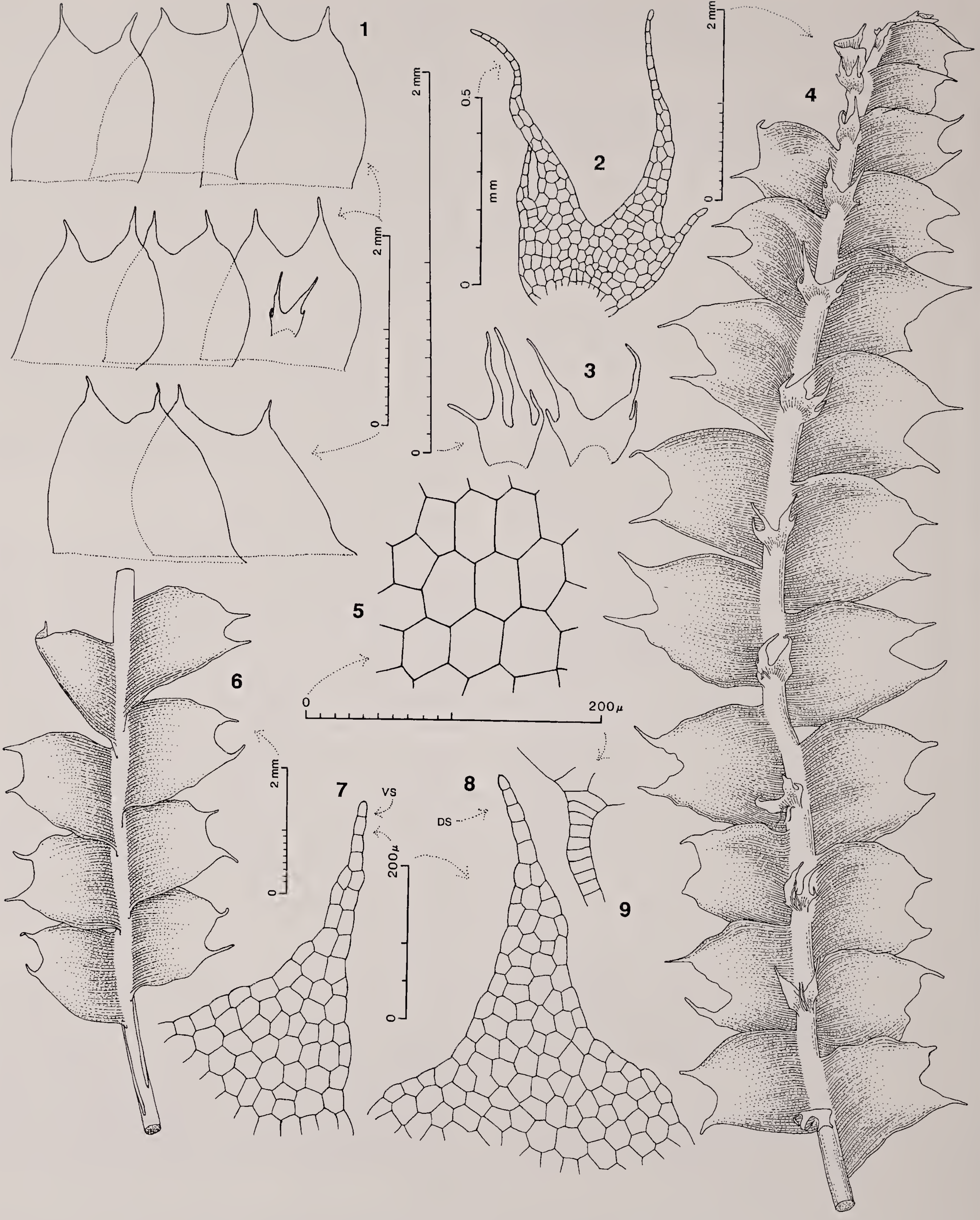

FIG. 21. *Chiloscyphus excisifolius* (Steph.) J. J. Engel & R. M. Schust. **1.** Leaves and within at middle right, an underleaf. **2.** Underleaf. **3.** Underleaves. **4.** Sector of main shoot, ventral view. **5.** Median leaf cells. **6.** Sector of main shoot, dorsal view. **7.** Portion of ventral segment (= vs) of leaf. **8.** Portion of dorsal segment (= ds) of leaf. **9.** Antheridial stalk. (All from type.)

Notes on Type Specimen—A few androecial shoots are present; the collection therefore is not sterile as mentioned in the protologue.

Distribution and Ecology—Known only from a few sites in Victoria and New South Wales, Australia. The type material, which has limited label data, was collected at "Hot Springs, Yarrangobilly Caves" (35°43′S, 148°30′E), in Kosciusko Natl. Park. At that location is a site known as Thermal Pool, which undoubtedly refers to the hot springs. I am unable to infer from label information whether the specimen was actually associated with hot springs, or if the reference to springs merely reflects location name and not niche.

The species also is associated with creeks in dry sclerophyll forests with sparse shrub cover of *Acacia*. It occurs on moist rock outcrops on creek banks.

Specimens Seen—**AUSTRALIA. VICTORIA:** Strawberry Gully, 70 km NE of Orbost, Bonang Highway, 700 m, *Streimann 10012*–c. ♂ (CBG). **NEW SOUTH WALES:** Bains Gully, 3 km S of Majors Cr., 780 m, *Streimann 27658* (NY).

Chiloscyphus anisolobus J. J. Engel & Glenny

Chiloscyphus anisolobus J. J. Engel & Glenny, Bryologist 111: 118. *f. 1, 2.* 2008. Holotype: New Zealand, Canterbury Prov., Waimakariri River, gorge of Taipoiti River, 1050 m, *Glenny 9736* (F); isotype: (CHR 583361).

Plants strongly anisophyllous, markedly soft, delicate, fragile, notably brittle, loosely creeping but becoming erect when in dense tufts, pale green to intense pure bright green, in life at times tinged with yellow-brown, distinctly nitid when dry, small, the shoots to 2.2 mm wide. Branching rather common, with intercalary branches frequent, variable in position, at times near ventral end of leaf above, some distance removed from an underleaf axil and somewhat ventral-lateral in position (then ?lateral intercalary), to occurring in underleaf axil and median-ventral in position (then ventral intercalary); *Frullania*-type branches also present, common. Stems with cortex poorly differentiated, the cortical cells in a single layer of cells ± similar in size to the medullary (especially ventrally) or a little larger, with walls thin, the exposed tangential wall weakly thickened; medullary cells thin-walled. Rhizoids inconspicuous, hyaline, in fascicles from stem at underleaf bases, the tips at times digitate. Leaves alternate, the orientation somewhat variable: ± horizontal to moderately dorsally assurgent, widely spreading, approximate to weakly imbricate, the orientation and insertion nearly horizontal, the insertion line nearly straight throughout and only feebly and gently arcuate at ventral end, the insertion not extending to stem midline dorsally and delimiting a leaf-free strip of 2 stem cells; leaves plane to feebly convex to weakly concave even on 1 axis, oblong-subrectangular to obovate-subquadrate, often widest at or above the middle, bilobed, but the leaves often with a process in distal sector of ventral margin that grades from a small to large tooth to a small lobe, and in the latter instances the leaves then trifid, the dorsal lobes always the largest, the dorsalmost sinus descending to 0.25–0.45 the total leaf length; lobes persistent, remaining ± complete, broadly acute to broadly and stoutly acuminate grading to apiculate, occasionally subcaudate, the lobe margins mostly entire but the dorsal at times with a tooth toward sinus base, the lobes terminating in a single cell or a uniseriate row 2–3(4) at most slightly elongate, thin-walled cells slightly to distinctly constricted at the septa, the distal sector of lobes submoniliform; dorsal margin of the lamina ± straight to moderately and gently curved, plane and neither inflexed nor deflexed, typically entire, sporadically with a tooth in median sector, the margin not or at most moderately decurrent; ventral margin with curvature much like the dorsal margin, plane, entire or with a process in distal sector (mentioned above), rarely with an accessory tooth in median sector. Cells notably thin walled, trigones completely lacking, the median cells 30–33(38) μm wide × 31–43 μm long; surface smooth. Oil-bodies in all leaf cells including those of lobes and marginal teeth, occupying moderate portion of cell lumen, dull grey at lower magnification, pale smoky grey at higher magnification, somewhat glistening, 4–9 per cell, conspicuously finely to moderately papillose, many subglobose, often elliptic, 6.7–7.2 × 5.3–5.8 μm to 10.1–11 × 5.3–6.2 μm, spherical 4.8–6.2 μm. Chloroplasts packed in cell (the plants intense green). Underleaves unistratose, only a small fraction of leaf area, ca. 1–1.5× stem width, free or very narrowly connate on 1 side (by 1–2 cells), the insertion crescent shaped; underleaves distant to contiguous, plane to weakly convex (ventral view), narrowly ovate-subrectangular to obtrapezoidal, bifid to ca. 0.6–0.8; lobes slenderly acuminate to attenuate-lanceolate, subparallel to diverging, 4–5(7) cells wide at base, then with several biseriate tiers, then terminating in a single cell or a uniseriate row of 2–3 (rarely 4) cells, the tip cell capped by a slime papilla, the lobe margins entire; lamina margins entire or on each side with a tooth to subciliiform process.

Asexual reproduction lacking.

Plants apparently dioecious; androecia unknown. Gynoecia infrequent, in a closely intertwined mass with perianths in close proximity to one another, fragile, strongly dorsally assurgent, with rhizoids at base, on lateral- and ventral-intercalary branches, as well as on innovations with a few cycles of small leaves prior to formation of bracts, the formation of a gynoecium with a short innovation occurring repeatedly. Bracts in 2–3 series, those of innermost series at times with dorsal margin fused in entirety with perianth, much larger than leaves, erect and ensheathing perianth throughout or appressed basally but with the lobes somewhat reflexed, the bracts free from one another, convex (dorsal view), narrowly ovate to elliptic; apex 2–3-lobed to 0.25–0.4, the lobes acuminate, plane or a little ventrally sulcate, entire or with a few teeth; dorsal margin of lamina with several teeth, often with a prominent acuminate to subulate appendage at the extreme base, the ventral margin with a lobule distally, which, when prominent, lends the bract 3-lobed, the margin otherwise with a few teeth and, at times an attenuate lacinia toward the base. Bracteoles of innermost series somewhat smaller, very narrowly connate on 1 side and free on the other, 4-lobed to 0.65–0.7, the lateral lobes narrower and shorter, the median lobe margins with 1–2-dentate-laciniate, the disc margins with a few small teeth. Perianth barely exserted beyond bracts, cyathiform, the younger ones in cross section terete throughout, the older ones becoming somewhat laterally compressed, but the keels rounded and never sharp, the perianth gradually becoming wider toward the shallowly 3-lobed mouth; lobes rather deeply bifid, the segments acuminate, entire or with 1(2) teeth, the lobes with a few accessory teeth, or laciniae or 1–2 lobules below the level of the segments; keelar wings lacking.

Sporophyte unknown.

Differentiation—This is a distinctive species that should offer no confusion with any other member of the genus. The soft, felt-like texture of the pale green to intense pure bright green plants is notable. The leaves are bilobed to 0.45, and often have accessory armature, but these are

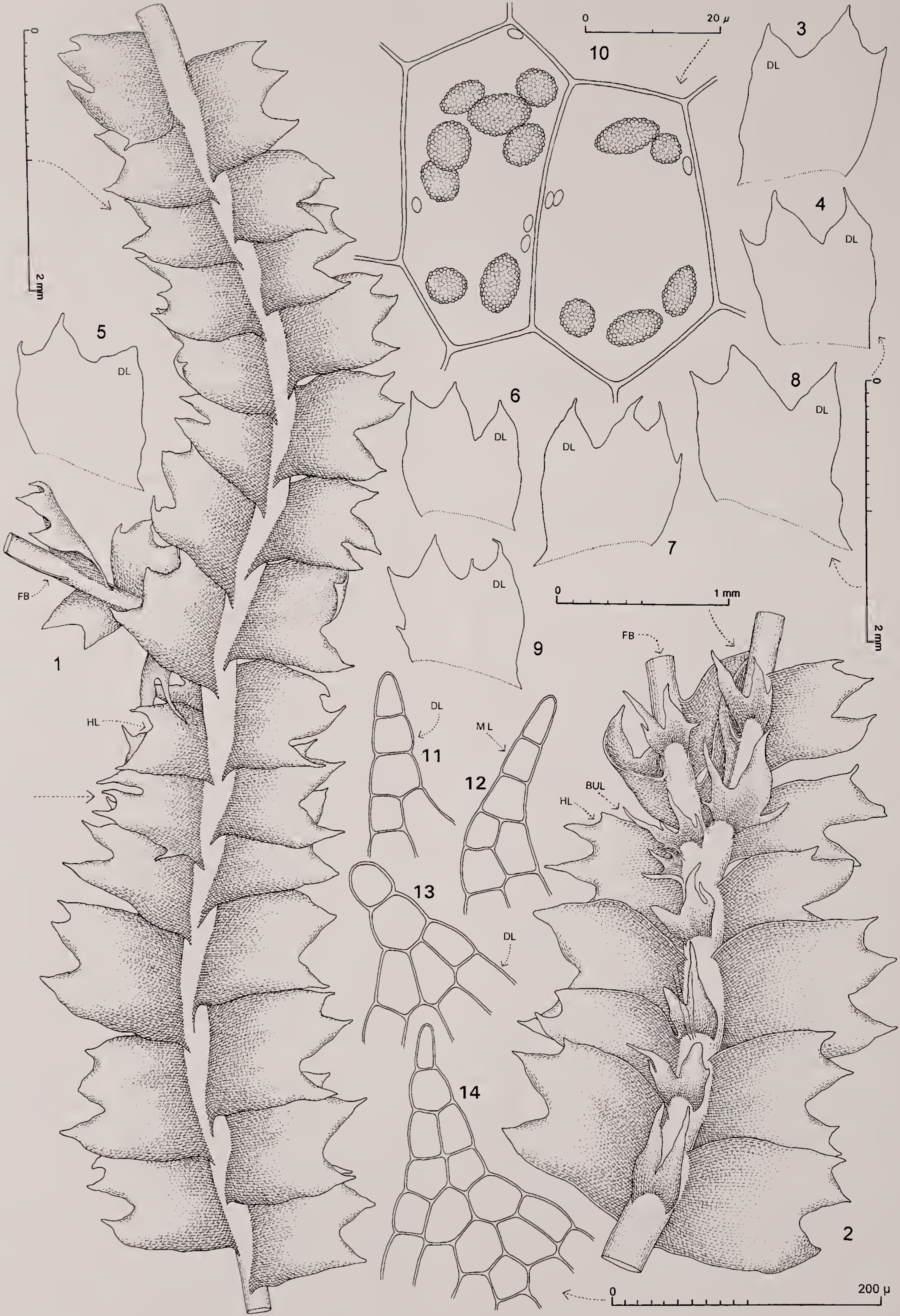

FIG. 22. *Chiloscyphus anisolobus* J. J. Engel & Glenny. **1.** Main shoot with *Frullania*-type branch (= FB; HL = half-leaf); note variability of leaf apices (dorsal view). **2.** Portion of main shoot with *Frullania*-type branch (= FB; HL = half-leaf), ventral view; note position of first branch underleaf immediately basal to first normal underleaf of branch (= BUL). **3–9.** Leaf outlines (all drawn to same scale). **10.** Median cells with oil-bodies. **11–14.** Distal sector of leaf lobes (dl = dorsal lobe; ml = "middle" lobe); all drawn to same scale. (All from holotype.)

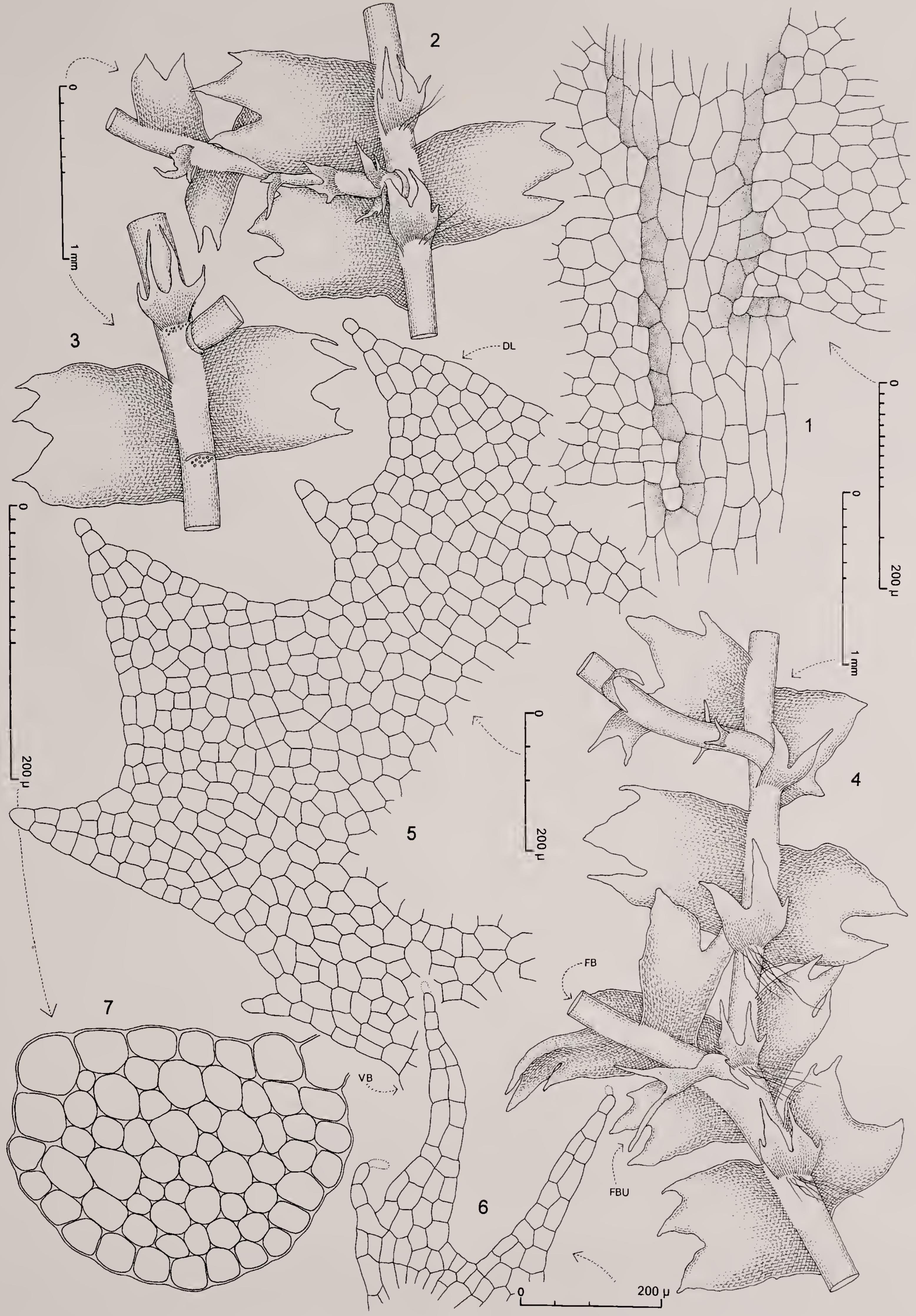

FIG. 23. *Chiloscyphus anisolobus* J. J. Engel & Glenny. **1.** Main shoot (dorsal view), showing that lines of leaf insertions do not extend to stem midline, with delimitation of a leaf-free strip of stem cells. **2, 3.** Sector of main shoot, ventral view; note position of intercalary branches. **4.** Portion of main shoot with intercalary branch issuing from middle of stem in underleaf axil (?ventral intercalary) and, lower, a *Frullania*-type branch (= FB; FBU = first branch underleaf), ventral view. **5.** Distal sector of leaf (dl = dorsal lobe; vb = ventral base of leaf); note teeth on dorsal lobe sinus margin and also on ventral margin of lamina. **6.** Underleaf. **7.** Stem, cross section. (All from holotype.)

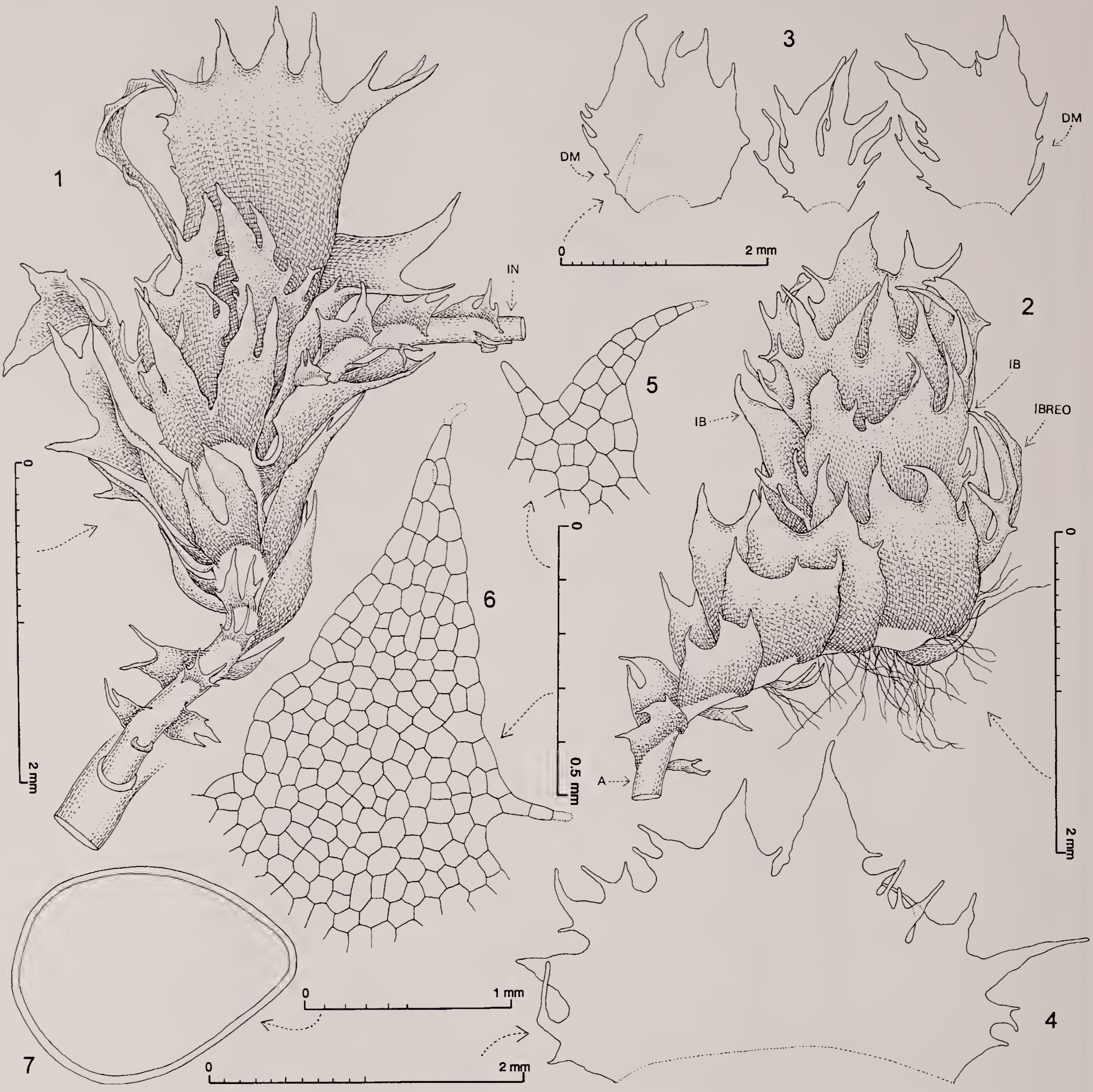

FIG. 24. *Chiloscyphus anisolobus* J. J. Engel & Glenny. **1.** Complete innovation terminating in a gynoecium (ventral view), a new innovation at right (= in). **2.** Innovation bearing a perianth (lateral view), which issues at a short distance below point A from a parent gynoecium-bearing innovation (IB = innermost bract; IBRO = innermost bracteole). **3.** ♀ Bracts and in middle, bracteole (dm = dorsal margin). **4.** Perianth mouth. **5, 6.** Lobes of perianth mouth. **7.** Cross section through median third of perianth. (All from *Engel 28583*, New Zealand, South Is., Western Nelson Ecological Prov., Kahurangi Natl. Park, Matiri Range, Thousand Acres Plateau.)

limited to rather specific loci. The distal sector of the ventral margin often has a process varying from a small to large tooth to a small lobe, and in the latter instances, the leaves are then trifid (Figs. 22: 1, 7; 23: 3). The dorsal lobe at times has a tooth toward the sinus base, but the leaf apices otherwise are devoid of accessory armature (Figs. 22: 9; 23: 5). The presence of a leaf-free strip of stem cells is also distinctive (Fig. 23: 1), a condition otherwise rare among our other species of the genus (see Engel 2004). Underleaves are at most 1.5× the stem width, free or very narrowly connate on 1 side, and bifid to ca. 0.6–0.8 (Figs. 22: 2; 23: 2–4, 6). The presence of a leaf-free strip and the underleaf form are similar to *Leptophyllopsis laxus*, but that species has caducous leaf lobes and apical teeth lending the leaf apices ragged (see Engel, 2007). Perianths have a distinctive aspect in the field. They are cyathiform (Fig. 24: 1, 2), and because the perianths are dorsally assurgent, the wide and open mouths are oriented toward the viewer.

Chiloscyphus anisolobus is similar to *C. excisifolius* of New South Wales, Australia, and shares the presence of a leaf-free strip of stem cells; distinctly bifid leaves; leaf cells notably thin walled and without trigones; underleaves about as wide as the stem to at most 1.5× the stem width; and a poorly differentiated stem cortex. For separation of the two species, see the key.

For additional comments see Engel and Glenny (2008a) and Engel (2007).

Distribution and Ecology—This species is known from several sites in Westland, Western Nelson, and Canterbury in the South Is. of New Zealand, and one station on the North Is.

The species is primarily known from scattered subalpine and alpine sites on South Is. It is locally common at the Gordon's Pyramid station, and occurred in a mosaic of tussocklands, occasional *Dracophyllum*, karst vegetation, bluff and scree communities, and exposed soil, set in a karst plateau landform. At this site plants formed large (15 × 30 cm), pure, loose, soft mats hanging from rock as well as on moist rock under vegetation cover deep in a small sinkhole. At the Temple Basin Ski Area occurring with *Marsupidium surculosum* on soil at the base of a very large exposed rocky outcrop near a stream. The type occurred at 1050 m in a steep river gorge, ca. 100 m deep, cut through greywacke (siltstone). The gorge walls are largely unvegetated but have isolated forbs such as *Chionochloa conspicua*, *Ourisia macrophylla*, and *Aciphylla similis*. The plants formed a mat ca. 30 × 50 cm at the back of a cave formed by a sloping rock ledge and a protecting overhang. Also known from ca. 790 m on predominately south-facing banks adjacent to a 30–40 m high vertical falls above a very humid, narrow stream system in a *Nothofagus menziesii* forest (Arthur's Pass, Avalanche Peak Track). At this site plants formed a ± pendent, weft-like, very soft and felt-like mat hanging parallel to rock but not attached to the rock under a low light in a protected pocket-like niche. The species occurs at much lower elevations in the Punakaiki area. On the south side of Porarari River (Paparoa Range, E of Punakaiki), plants occurred at 10 m, loosely creeping over a thin soil layer on a shaded limestone ledge in a limestone gorge. The site is within a dense lowland forest dominated by *Rhopalostylis sapida*, *Dicksonia squarrosa*, *Cyathea* sp., *Coprosma* spp., and *Freycinetia banksii* with scattered *Podocarpus* and *Metrosideros*. The Fife plant (*4719*) occurred at 30 m over a south-facing mesic limestone face at the margin of a vehicle track (gorge of Bullock Creek, 1.2 mi. E of Route 6). Known from a single North Is. station, at ca. 700 m, in a mosaic of scattered rocky outcrops, patches of *Nothofagus menziesii* and open areas with liverworts, mosses, and herbaceous and low-growing woody angiosperms (Tree Trunk Gorge, W bank of Tongariro River).

Specimens Seen—**NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.:** Paparoa Range, S side of Porarari River in limestone gorge, E of Punakaiki, 10 m, *Engel 19153* (F); Punakaiki area, gorge of Bullock Creek, 1.2 mi. E of Route 6, 30 m, *Fife 4719* (F); Arthur's Pass Natl. Park, Upper Otira Valley, 1035–1160 m, *Fife 5925* (F). **CANTERBURY PROV.:** Arthur's Pass Natl. Park, Arthur's Pass, Falls behind Department of Conservation Station, off Avalanche Peak Track, ca. 790 m, *Engel & von Konrat 27234* (F); ibid., Temple Basin Ski Area, vicinity between Temple and Cassidy basins, ca. 1500–1600 m, *Engel & von Konrat 28475* (F). **WESTERN NELSON:** Kahurangi Natl. Park, Garibaldi Ridge, immediate vicinity and at peak of Gordon's Pyramid, ca. 1280–1380 m, *Engel & von Konrat 27125* (F); Kahurangi Natl. Park, Matiri Range, Thousand Acres Plateau, ca. 1100–1200 m, *Engel & von Konrat 28583* (F). **NORTH ISLAND. WELLINGTON PROV.:** Tree Trunk Gorge, W bank of Tongariro River, E border of Tongariro Natl. Park, boundary of Kaimanawa State Forest Park, ca. 700 m, *Engel 21198* (F).

Chiloscyphus perpusillus (Hook. f. & Taylor) J. J. Engel

Jungermannia perpusilla Hook. f. & Taylor, London J. Bot. 3: 380. 1844. *Lophocolea perpusilla* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 163. 1845. *Chiloscyphus perpusillus* (Hook. f. & Taylor) J. J. Engel, Contr. Univ. Michigan Herb. 18: 110. 1992. Lectotype (*nov.*): Campbell Is., Nov. 1840, *Hooker* (FH!); isolectotypes: (BM![4], S![2], W!).

Lophocolea decolorata Steph., Bull. Herb. Boissier 6 (10): 875. 1906 (= Spec. Hep. 3: 100), *syn. nov. Chiloscyphus decoloratus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 414. 1985 (1984). Type: Tasmania, Mt. Wellington, St. Crispin's Well, 23 Dec. 1895, *Weymouth 592* (G!–c. per. + young ♀).

Lophocolea macroloba Steph., Bull. Herb. Boissier 6(10): 876. 1906 (= Spec. Hep. 3: 101), *syn. nov. Chiloscyphus macrolobus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 418. 1985 (1984). Lectotype (*nov.*): Tasmania, Mt. Wellington, St. Crispin's track, 24 Jan. 1899, *Weymouth 1548* (G!–c. ♂ + young ♀); isolectotype: (HO!).

Lophocolea brevis Steph., Spec. Hep. 6: 265. 1922, *syn. nov. Chiloscyphus brevis* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 412. 1985 (1984). Lectotype (*nov.*): Tasmania, West Coast, Dubbilbarril, Mt. Lyell, railway, 30 Dec. 1899, *Weymouth 969* (G!–c. per.); isolectotype: (HO!).

Plants with a superficial resemblance to *Geocalyx*, rather fragile, loosely prostrate, pale green; shoots small, to 2.2 mm wide. Branches common, all or mostly of *Frullania* type (the half-leaf usually undivided but sporadically bifid and then the ventral lobe larger than the dorsal); lateral-intercalary branching occasional to rather common, from ventral-lateral sector of stem ca. midway between two underleaves or in lateral half of underleaf axil. Stems narrow for plant size, 8–9 cells high, the cortex poorly differentiated, in a single layer of cells feebly smaller than those of medulla, the cortical and medullary cells both thin walled. Rhizoids in fascicles from stem at immediate base of underleaf, the tips often branched. Leaves alternate, distinctly dorsally assurgent at least in basal sector, widely spreading, loosely imbricate, free or sporadically connate dorsally, orientation strongly succubous, the insertion not to slightly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the insertions of opposing leaves often extending to the dorsalmost laterally juxtaposed rows of stem cells and not to exact midpoint of stem. Leaves slightly convex, subsymmetrically ovate (at times narrowly so and grading toward subelliptic) to ovate-subtrapezoid, widest near base or at a point 0.3–0.4 from base; apex bifid to 0.2–0.3, the lobes often incurved, ± parallel to diverging, plane to somewhat ventrally sulcate, subequal, ranging from narrow to wide acute, often subacuminate, young leaves with lobes distinctly acuminate and terminating in a uniseriate row of at least 5 cells, the cells usually wider than long but occasionally are isodiametric or slightly longer than wide, the uniseriate row of cells caducous within a few gyres from shoot apex, the adult leaves with lobes terminating in 2(3) laterally juxtaposed cells that frequently possess secondary septa, the abscission of uniseriate row occasionally incomplete and the basal cell of row remains, the lobe margins entire or occasionally with a tooth, the sinus often lunate; dorsal margin straight to slightly rounded, plane, usually entire, very rarely with a tooth, decurrent; ventral margin broadly and gently curved, much like the dorsal in extent of curvature or the ventral somewhat more strongly curved, plane, entire or (frequently) with a broad-based tooth. Leaf cells with walls thin, trigones normally medium to large to ± knot-like, atypically minute, at times more pronounced in basal half of lobes, median leaf cells 16–26 μm wide, 19–29 μm long; surface smooth. Oil-bodies 2 or 2–3 per cell, the surface coarse. Underleaves much smaller than leaves, 1–1.9× stem width, usually free but in suboptimal plants sporadically narrowly connate by 1–2 cells on 1 side, insertion often asymmetric, crescent shaped, the underleaves varying from ± parallel with stem to widely spreading, distant to approximate, plane to slightly convex (ventral view) sometimes feebly concave but never consistently so, sporadically but never consistently concave, obtrapezoid, bifid to at least 0.65 and defining a lamina 2–6 cells high; lobes mostly diverging, sporadically ± parallel, acuminate to subcaudate, plane or faintly ventrally sulcate, the lobe margins entire or with a tooth; lamina margins plane to slightly reflexed, entire or with a process ranging in size from a tooth to a lacinium, the armature somewhat variable in position: basal or slightly distal to level of sinus base.

Asexual reproduction by caducous leaf lobe tips, by regeneration from adult leaves, *in situ*, or by gemmae produced at the lobe tips or from regenerants, the gemmae 2-celled and 19–25 × 11–12 μm to less often 4-celled and 22–46 × 12–13 μm.

Plants dioecious. Androecia on leading shoots or elongate, indeterminate, *Frullania*-type branches, occasionally on lateral-intercalary branches or, rarely (1 branch seen), on ventral-intercalary branches that lack vegetative leaves basal to bracts but proliferate vegetatively distally, the androecia subfolious; bracts slightly to moderately smaller than leaves, often similar in shape and size to vegetative leaves except for development of a lobule, the bracts suberect to spreading, strongly dorsally assurgent, loosely appressed to bract immediately above, the saccate portion crenulate in profile and fused toward base with opposite bract, the apex as in leaves, the ventral margin entire; lobule margin involute, with a distinct distal rounded or tooth-like projection, the margin otherwise crenate-denticulate and with copious slime papillae; antheridia solitary, the stalk to 30 cells long, uniseriate. ♂ Bracteoles often connate on 1 side, often less deeply bifid than underleaves (sometimes divided to only 0.5). Gynoecia ± isophyllous, on main shoot, or on lateral-intercalary branches varying from short and without normal leaves to long, or on subfloral innovations that originate from axil of innermost bract or those of second series. Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free from one another, convex, ovate, rather strongly narrowed distally; apex bifid to 0.3, the lobes subcaudate-caudate, ventrally sulcate, entire or sporadically with a tooth; lamina margins reflexed, the dorsal often strongly and sharply so, the margins entire or with a few teeth. Bracteoles of innermost series similar to bracts in size, free or narrowly connate on 1 side, concave to distally subcanaliculate, similar to bract shape or obovate; apex bifid to 0.35, the lobes similar to those of bracts; lamina margins reflexed, entire or with 1–2 teeth or laciniae. Perianth seldom produced, long-exserted beyond bracts, sharply trigonous throughout, narrowly oblong, not narrowing toward the rather deeply 3-lobed mouth; lobes distinctly bifid, the segments acuminate to subcaudate, entire or with a tooth, the lobes spinose dentate to laciniate below level of segments; keels sharp, with keelar wings common, rather high, with laciniae common.

Seta seen only in collapsed state. Capsule wall 35–38 μm thick, of 4 layers, the outer layer of cells exceeding thickness of all combined interior strata; outer layer of cells irregularly quadrate, the radial walls thin, with red-brown nodular to feebly spine-like thickenings mostly on longitudinal walls and only sporadically on transverse walls, the exposed tangential wall thickened; intermediate and inner layer of cells subequal in thickness; innermost layer of cells irregularly short rectangular, the vertical radial walls with somewhat thick continuous sheets of red-brown wall material, with semiannular bands red brown, common, wide, close and numerous, sometimes incomplete, often forked and anastomosing to delimit fenestrae, the radial walls with nodular to spine-like thickenings sometimes present on both longitudinal and transverse walls.

Spores and elaters not seen.

DIFFERENTIATION—This species is at once distinct from other members of sect. *Lophocolea* in having caducous leaf tips (Fig. 26: 6, 7) and, together with *C. erosus*, are the only species in the section that produce gemmae (Fig. 26: 4, 5). The form of the leaf (distinctly bilobed and often ovate-elliptic) and underleaf (reduced lamina height and 2 prominent lateral processes) also occurs in *Chiloscyphus lentus*, and confusion may occur with that species. *Chiloscyphus lentus*, however, has persistent leaf tips, underleaves consistently connate on one side, uniformly entire-margined leaves, and, on the whole, smaller trigones, being minute to small or at most medium and straight sided. *Chiloscyphus perpusillus* normally has free underleaves (Fig. 25: 1), ventral leaf margins often 1-dentate and trigones normally at least medium and straight sided and often large and bulging (Fig. 25: 4).

The closest relative to *C. perpusillus* among underleaf-free species is *C. bispinosus*, which is unknown for Tasmania but common in New Zealand. The two species have well-developed trigones, similar cell size, and deeply divided underleaves (though the range is shallower in *C. perpusillus*). *Chiloscyphus bispinosus* is at once distinct in having bordered leaves and persistent leaf lobes.

Asexual reproduction in *C. perpusillus* occurs via caducous leaf lobe tips, gemmae, and regeneration from *in situ* adult leaves (Engel, 1993). The uniseriate row of cells of both lobes breaks from the parent plant within a few gyres of the shoot apex, and, consequently, complete lobes are rare (Fig. 25: 1, 3). Secondary cell wall division, as the presumed precursor to regenerant and gemmae formation, may be seen on young leaves (Fig. 26: 2) as well as at the tips of that portion of the lobe remaining on adult leaves (Fig. 26: 6, 7), and the frequent presence of such very thin secondary walls is a good taxonomic character for the species. Remarkably, regenerants, even when young, produce gemmae (Fig. 26: 4), a feature unique for Hepaticae (see Engel, 1993). Also, remarkably, gemmae may be produced from leaf lobe tips of juvenile plants, as in *Ratkowsky 79/45* from Tasmania. The form of the lobe tips of adult leaves is diagnostic for the species, and consists of 2–3 laterally juxtaposed cells, each rounded at the free end (Fig. 26: 6, 7). Such consistently nonragged lobe apices indicate that gemmae production is limited. The basal sector of the leaf lobes remains intact and the intervening sinus is always present. In this respect *C. perpusillus* differs from *C. erosus*, in which gemmae formation is copious and probably continuous, resulting in the entire distal sector of the leaf becoming erose, with disappearance of lobes and ultimately the sinus.

Chiloscyphus perpusillus bears a superficial resemblance to *Geocalyx caledonica*, which also occurs in Tasmanian forests. If sterile plants are at hand the smooth leaf surface and caducous leaf tips of *C. perpusillus* will immediately resolve any ambiguity; *G. caledonica* has a coarsely striate-papillose surface and persistent leaf tips.

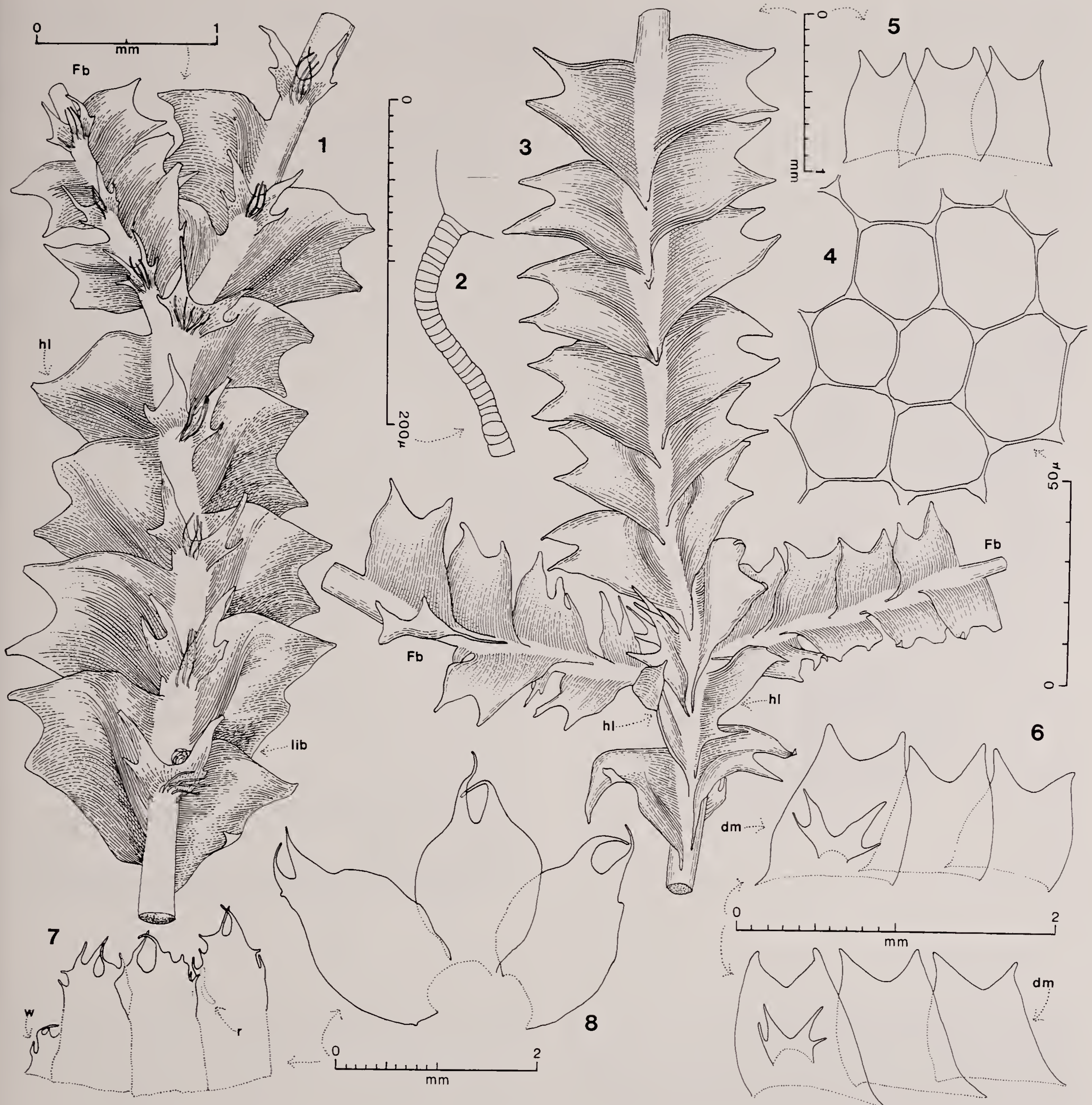

FIG. 25. *Chiloscyphus perpusillus* (Hook. f. & Tayl.) J. J. Engel. **1.** Sector of main shoot, ventral view, with *Frullania*-type branch (= FB; HL = half-leaf); note form of 1st branch leaf and position of very young lateral-intercalary branch (= LIB) in lateral half of axil of basalmost underleaf. **2.** Antheridial stalk. **3.** Sector of leading shoot with 2 *Frullania*-type branches (= FB; HL = half-leaf) (dorsal view); note 3-lobed leaf on main shoot just distal to left branch and an additional one on left branch. **4.** Median leaf cells. **5.** Leaves from same shoot, note subsymmetrical shape. **6.** Leaves and underleaves from same shoot, top 3 all with dorsal margin (= dm) at left, bottom 3 all with dorsal margin (= dm) at right. **7.** Perianth mouth, ventral lobe in middle (r = regenerant from inner face; w = wing) **8.** ♀ Bracts and in middle, bracteole. (**1, 4, 6,** from *Norris 28684*, Tasmania, Mt. Field Natl. Park, Lake Belcher; **2,** from *Engel 16349*, Tasmania, Mt. Rufus Canal Road; **3,** from *Norris 29292*, Tasmania, Mt. Wellington, McRobies Gully; **5,** from *Engel 12804*, Tasmania, Hartz Mtn. Natl. Park, Devils Backbone; **7, 8,** from *Engel 19467*, Tasmania, Griffiths Creek, ESE of Mt. Arrowsmith.)

A rare phase of this species may have teeth, one each on the dorsal and ventral margins, the sinus, and the outer margin of the lobe, lending a somewhat ragged appearance (examples are *Rodway s.n.* from Cascades, Tasmania, and *Rodway s.n.* from Sandfly, Tasmania). Both collections are suboptimal, and perhaps presence of such ornamentation is restricted to suboptimal plants. This phase has copious gemmae production.

Such rare phenotypes should not be confused with *Leptophyllopsis laxus*, which also has caducous leaf lobes.

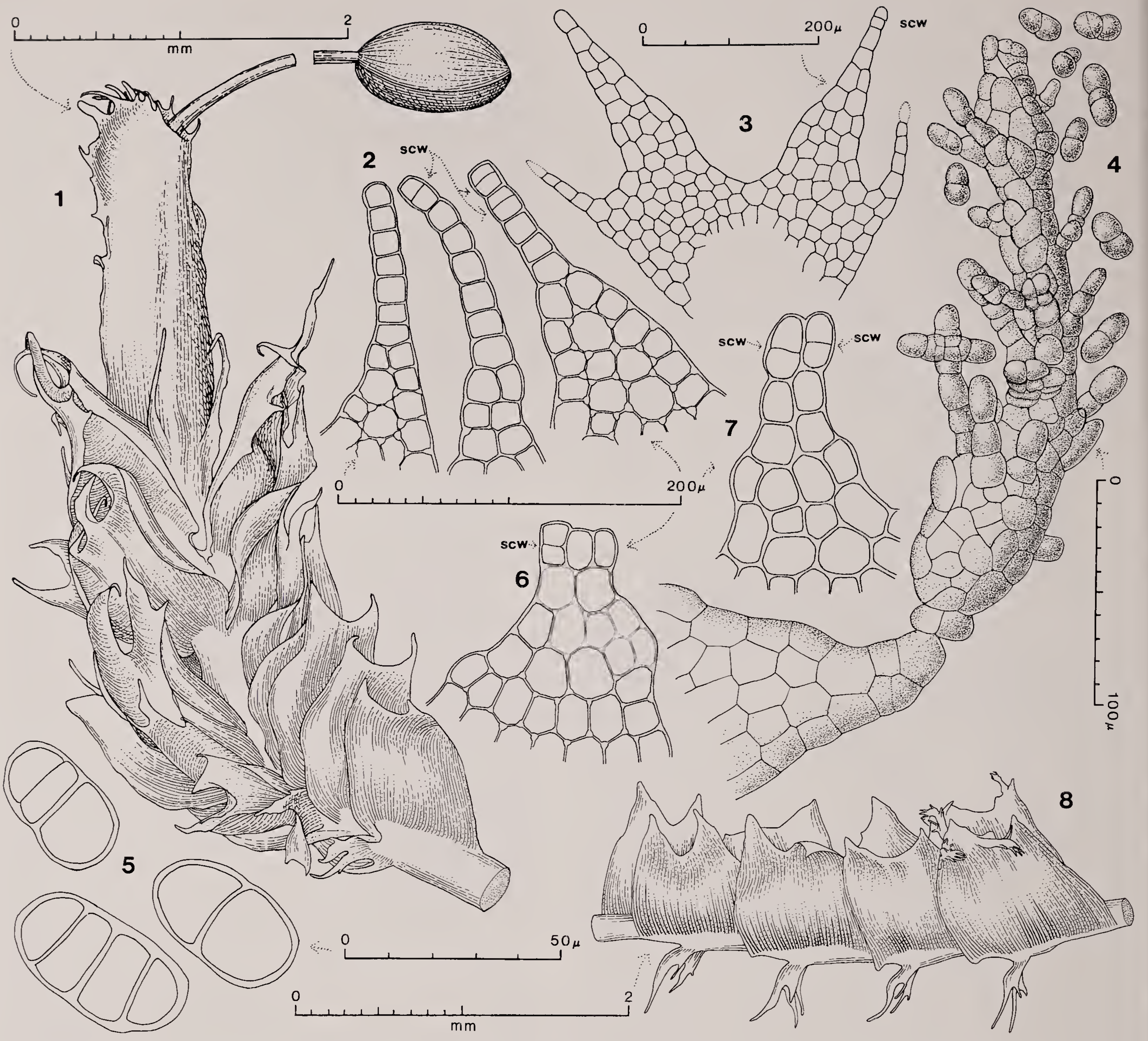

FIG. 26. *Chiloscyphus perpusillus* (Hook. f. & Tayl.) J. J. Engel. **1.** Mature isophyllous gynoecium (note 2 laciniiform processes toward perianth base), ventral-lateral view. **2.** Distal sectors of 3 segments of young leaves, all from same shoot; note precocious secondary cell wall development (= scw). **3.** Underleaf. **4.** Apex of leaf segment showing gemmae producing regenerant; note 2–4 celled gemmae. **5.** Gemmae (all to same scale). **6, 7.** Distal sectors of segments of adult leaves, the uniseriate row having been lost; note secondary cell wall formation in distalmost cells. **8.** Sector of main shoot showing regeneration from leaves (on 2 basalmost opposing leaves), lateral view. (**1, 4, 5,** from *Engel 19467*, Tasmania, Griffiths Creek, ESE of Mt. Arrowsmith; **2, 3, 6–8,** from *Norris 28684*, Tasmania, Mt. Field Natl. Park, Lake Belcher.)

The two species, though rarely, may be intermixed. *Leptophyllopsis* is larger, translucent, and has much larger leaf cells that are completely devoid of trigones. Also, *Leptophyllopsis* does not produce gemmae.

This phenotype, when rather small, may offer confusion with *Clasmatocolea inflexispina*, which also has well-developed trigones and free underleaves. That species may be immediately separated by persistent leaf lobes and absence of secondary cell walls.

VARIATION—Trigones are usually medium and straight sided to large and convex sided (Fig. 25: 4). However, occasional populations have trigones varying from minute to large and bulging; I have seen shoots with some leaves possessing minute trigones, whereas other leaves have trigones medium and straight sided (*Engel 19467*).

Underleaf orientation and concavity are variable. Underleaves may be ± parallel with the stem to widely and stiffly spreading, and the disc varies from plane to concave. Leaves that are stiffly spreading often are also concave (Fig. 26: 8). Underleaves are either uniformly plane or occur as a mixture of plane and concave individuals (they are never consistently concave).

NOTE—Interesting tendencies occur on androecium-bearing plants. The bracteoles are often connate on one side and often less deeply divided, at times bifid to only 0.5. Underleaves on sterile shoots, on the other hand, are free and uniformly deeply divided. ♂ Bract lobes, however, show little differentiation from vegetative leaves, and in side view (the predominent view of the shoot in that both ♂ bracts and leaves are usually dorsally assurgent) the bracts are hardly distinguishable from vegetative leaves.

NOTES ON TYPE SPECIMENS—1) *Jungermannia perpusilla* Hook. f. & Taylor The protologue states Campbell Is. for locality, that the plants are ascending and occur "on different *Musci*," and also that androecia and gynoecia are present. I have seen plants from both Campbell and Auckland Islands. Several Campbell Is. plants collected by Hooker on loan from BM and FH appear to be segregates of a single specimen consisting of ascending shoots intermixed with *Metzgeria* sp., *Clasmatocolea strongylophylla* (Hook. f. & Taylor) Grolle, a Lejeuneaceae, numerous fern sporangia and an isolated moss. The FH specimen has a glued tuft labeled "perichaetia." These consist of young perianths in the early leaf-fusion stage that do not extend beyond bracts, and are the "barren perichaetia" referred to in the protologue. The FH collection also has two shoots mounted between small pieces of plastic; the shoots are androecial and closely match the protologue. I found only a few young perianths and no androecia among BM specimens. Campbell Is. plants are rather flaccid and on some shoots secondary cell walls are present but comparatively sparsely developed, as typically occurs in flaccid material. Other shoots have secondary cell walls rather frequent and with continued gemmae formation the lobes may become rounded. A sinus is nearly always present and accessory lobes are lacking. Such erose lobes are exceptional for the species, and the extreme of this feature is attained in the type. Very rare and isolated leaves have continued gemmae production to the extent that the entire leaf apex is rounded and a sinus is lacking. Leaves are strongly dorsally assurgent, and leaf lobe tips appear much like Fig. 26: 6, 7, except secondary cell walls are only sporadic. Isolated (2-celled) gemmae are present. Trigones are mostly medium and straight sided to occasionally large and somewhat bulging. Underleaf margins are plane to slightly recurved, and the disc is plane to feebly concave. Branching is mostly terminal. I selected the FH specimen as lectotype. The lectotype has gemmae producing regenerants similar to Fig. 26: 4.

Two specimens collected by Hooker from Auckland Island at FH appear sterile; one is pure, the other is mixed with *Kurzia* sp. Both collections are somewhat flaccid but secondary cell walls are clearly demonstrable on less flaccid shoots; gemmae are frequent. Trigones are medium to large. Both specimens are *C. perpusillus*. A Hooker specimen at BM labeled Auckland Is. is confusing. It has several tufts with shoots intermixed with *Metzgeria* sp., fern sporangia and a Lejeuneaceae, thus matching Campbell Is. plants. Yet glued tufts of primarily *Kurzia* are also present. Because plants of this genus were seen only in Auckland material, it is clear that the several pieces of the Campbell Is. element were mistakenly mounted with Auckland Is. plants. A Hooker isolectotype mistakenly labeled Auckland Island is also at S.

2) *Lophocolea decolorata* Steph. The lower shoot sectors are somewhat flaccid, and here cell walls are irregular and trigones minute. Stephani must have examined such a shoot sector when stating that trigones are lacking. Distal sectors of shoots, however, have nonflaccid leaves with distinctly knot-like trigones. Secondary cell walls are common and gemmae are present. Underleaves are free at least on vigorous shoots; they are not connate on 1 side as stated in the protologue. Androecia and young gynoecia are present; the latter are in the early leaf-fusion stage and included within subtending bracts.

3) *Lophocolea macroloba* Steph. Androecial shoots are abundant, and at times they grow in close association with shoots having young gynoecia (early leaf-fusion stage and included within bracts). No physical connection occurs between male and female plants—the plants are therefore not monoecious as stated in the protologue. Trigones are variable, even on a single shoot, ranging from small on leaves toward the shoot base to medium and ± knot-like on leaves of median and distal sectors of shoots. Stephani erroneously stated trigones are lacking. Secondary cell walls are common and gemmae are present. Specimens at G and HO bear the same label information except for number. The specimen at G is number 1548, whereas that at HO is 519. The HO collection has the note "determ'd Stephani (n. 1548)" and is therefore part of the type collection. The HO specimen has a ± mature perianth among the many shoots bearing young gynoecia.

4) *Lophocolea brevis* Steph. Plants are quite flaccid, and lower shoot sectors are particularly so, having ± collapsed cells with irregular cell boundaries and small trigones. Well-formed leaves, especially those on distal sectors of shoots, have trigones medium and straight sided to large and slightly to moderately bulging. Secondary cell walls are difficult to demonstrate and perhaps are lacking on lower shoot sectors with flaccid leaves. However, such walls are present on distal nonflaccid leaves. Gemmae are present. Leaves are mostly entire, but the dorsal margin sporadically has a tooth. A few perianths are present.

DISTRIBUTION AND ECOLOGY—Known from New Zealand: Campbell and Auckland Islands, Stewart Is., South Is. (sea level + 720 m), and Tasmania (100–1225 m).

The species is relatively common in Tasmania, where it occurs in various wet forest niches. It occurs on bark of trees or exposed roots, on moist, shaded, sometimes bryophyte-covered logs and on earth (in moist gullies). It also may be present in niches associated with watercourses, such as on soil of river or stream banks, and, occasionally, on rock of creek beds. In the subalpine zone the species may be found on soil under shrub cover and in boulder crevices where soil has accumulated.

The species is very rare in New Zealand and is known only from one station on Stewart Is. and two on South Is. In the Martin's Bay area (Fiordland), the species occurred on a mossy bank at the forest edge near the seashore. Also known from 720 m in Mt. Cook Natl. Park within the scrub–*Nothofagus menziesii* transition zone, where the species occurred mixed with *Clasmatocolea inflexispina* on soil of an exposed slope. At Port Pegasus, Stewart Is., plants occurred in a podocarp/hardwood forest including *Prumnopitys ferruginea* and *Weinmannia racemosa*.

SPECIMENS SEEN—**AUCKLAND IS.:** *Sin. coll.* (BM, S); *Hooker s.n.* (FH, S). **NEW ZEALAND. STEWART ISLAND:** Port Pegasus, sea-level to ca. 70 m, *Engel, von Konrat & Braggins 24222A* (F). **SOUTH ISLAND. OTAGO:** Fiordland Natl. Park, Martin's Bay, N of McKerrow River, *Hatcher 1047* (F). **CANTERBURY:** Mt. Cook Natl. Park, SW-facing cliffs off Wakefield Track, overlooking Hooker River, E of town of Mt. Cook, 720 m, *Engel 18180B* (F). **TASMANIA.** Hartz Mtn. Natl. Park, Devils Backbone, above Lake Perry and Lake Osborne, 960–1020 m, *Engel 12804*–c. ♂ (F); along Arve Road, about 0.5 mi. E of Willies Saddle, ca. 350 m, *Norris 29866* (F); Arve Valley, Arve Loop Road, near junction with Arve Road, N of Hartz Mtn. Natl. Park, 150–200 m, *Engel 12840*–c. ♂ (F); along Huon River, near Blakes Opening, ca. 150 m, *Norris 30122* (F); Sandfly, *Rodway s.n.* as *L. lenta*–c. ♂ (HO); Mt. Wellington, Pipeline

Track, *Ratkowsky 79/94* as *L. lenta* (HO); ibid., Wellington Falls Track, Sandstone Gutter, ca. 670 m, *Ratkowsky s.n.* as *L. subporosa* (F); ibid., St. Crispin's, *Weymouth 111* as *L. erectifolia*–c. ♂, *519* as *L. macroloba* (HO); ibid., Watchorn's Creek, *Weymouth 495b* as *L. bridelii* (FI); ibid., Deep Creek (= Long Creek), *Weymouth s.n.* as *L. erectifolia*–c. ♂ (HO); ibid., near Silver Falls, *Ratkowsky 78/127* as *L. lenta* (HO); ibid., Silver Falls, ca. 610 m, *Ratkowsky s.n.* as *L. lenta*–c. sporo. (F); ibid., The Springs, *Ratkowsky s.n.* as *L. lenta* (F); ibid., O'Gradys Track, 600 m, *Ratkowsky 77/145* (HO); ibid., McRobies Gully, ca. 100–300 m, *Norris 29292* (F); ibid., Thark Ridge, *Ratkowsky s.n.* as *L. lenta* (F); ibid., Sphinx Rock Track from Summit Road, *Ratkowsky s.n.* as *L. lenta* (F); ibid., near Lone Cabin, *Ratkowsky s.n.* as *L. lenta* (F); Mt. Wellington Range, Trestle Mtn., *Ratkowsky 78/139* (HO); Myrtle Forest, SW of Collinsvale, ca. 2.3 km N of Collins Bonnet, 700 m, *Engel 12767* (F); summit area of Collins Cap, SW of Collinsvale, 1050 m, *Engel 13170* (F); Mt. Field Natl. Park, *Ratkowsky 78/125* as *L. lenta* (HO); ibid., near Lake Dobson, *Ratkowsky 78/126* as *L. lenta* (HO); ibid., Lake Belcher, ca. 900 m, *Norris 28634*–c. ♂ (F); plateau region E and SE of Mt. Eliza summit, E of Lake Pedder, ca. 1225 m, *Engel 13675* (F); Gordon River, *Weymouth 1481* as *L. macroloba*–c. ♂ (HO); Derwent Bridge, near Lake St. Clair, ca. 720 m, *Selling 53* as *L. bispinosa* (S); Cradle Mtn.–Lake St. Clair Natl. Park, terminus of Mt. Rufus Canal Road, S of Mt. Rufus and Lake St. Clair, 750 m, *Engel 16349*–c. ♂ (F); ibid., Mt. Rufus, *Ratkowsky 78/131* (HO); Griffiths Creek, tributary of Surprise River, ESE of Mt. Arrowsmith, 1.7 km via Lyell Highway W of King William Saddle, 17.4 km W of Derwent Bridge, 700–720 m, *Engel 19467*–c. sporo. + ♂ (F); Dubbillbarril, Mt. Lyell Railway, *Weymouth 970* as *L. decolorata* (F, HO); ibid., King River, *Weymouth 1434* as *L. bidentata* (HO); Rinadeena, Mt. Lyell Railway, *Weymouth 901* as *L. macroloba* (HO); Cradle Mtn.–Lake St. Clair Natl. Park, near Waldheim Chalet, *Ratkowsky 79/45* (F); ibid., Cradle Mtn., *Rodway s.n.* as *L. lenta* (HO); ibid., Cradle Valley, *Rodway s.n.* as *L. fissistipula* (HO); ibid., near Pencil Pine Lodge, about 5 mi. N of Cradle Lake campground, *Norris 34162* (F); Paddys Lake, below and E of Black Bluff, SW of Nietta, 1090 m, *Engel 19780* (F); White Timber Mtn., ca. 640 m, *Ratkowsky 77/149* as *L. lenta* (HO).

Chiloscyphus erosus J. J. Engel

Chiloscyphus erosus J. J. Engel, Phytologia 83: 43. 1998 (1997). Holotype: New Zealand, North Is., South Auckland Prov., Plateau E of Waiotapu Valley, ca. 1800 ft, *Allison 3569* (CHR!).

Plants rather stiff and wiry, the shoots initially suberect to erect, often undulate, but often ultimately cernuous, often becoming flagelliform toward the tip, the basal portion often ultimately leafless with age, the plants pale green; shoots to 0.8 mm wide. Branches common, all or mostly intercalary: lateral somewhat more common than ventral; *Frullania*-type branching rare and sporadic. Stems fleshy and large for plant size, 8–10 cells high, the cortex poorly differentiated, in a single layer of cells feebly smaller than those of medulla, the cortical and medullary cells both very thick walled. Rhizoids in fascicles from stem at immediate base of underleaf. Leaves alternate, distinctly dorsally assurgent, widely spreading, loosely to rather closely imbricate, free dorsally, orientation strongly succubous, the insertion not to slightly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves plane to slightly concave, subsymmetrically broad ovate to suborbicular to feebly oblate, widest in median sector; apex of well-developed leaves short bifid to retuse-bidentate, the lobes ± parallel, plane to sporadically feebly ventrally sulcate, subequal, apiculate to acute and with a uniseriate row of a few to several cells, but with gemmae formation, the lobes becoming blunt to rounded and progressively reduced until entire distal part of leaf erose and the lobes all or mostly disappearing, the leaf apex then broadly rounded; lobe margins, when present, entire or sparingly denticulate; dorsal margin broadly and gently curved, plane, entire or with a tooth; ventral margin broadly and gently curved, much like the dorsal in extent of curvature or the ventral somewhat more strongly curved, plane, commonly with 1 to several teeth, occasionally entire. Leaves in distal sectors of shoots often smaller and less well developed, often with 1–2 accessory lobes and then often appearing 3–4-lobed, freely gemmiparous, lending the whole leaf a ragged 3–4-lobed appearance. Leaf cells with walls thin, trigones medium to large, with sides straight to somewhat bulging, median leaf cells 16–20 μm wide, 17–25 μm long; surface smooth. Underleaves much smaller than leaves, ca. 1–1.4× stem width, free or narrowly connate on 1 side, insertion crescent shaped, the underleaves normally varying from ± parallel with stem to moderately spreading, distant to contiguous, plane to somewhat convex (ventral view), elliptic to narrowly ovate, the sinus depth variable, some populations bifid to 0.25–0.6, other populations bifid to 0.7–0.9; lobes parallel to diverging, acuminate, plane, the lobe margins entire or with a tooth; lamina margins plane, entire or with a dentiform to ciliiform to laciniiform process.

Asexual reproduction by gemmae, which are uniformly developed and abundantly produced, the gemmiparous leaves becoming abnormal and progressively more erose margined; gemmae 2-celled, 25–28 × 16–17 μm.

Plants dioecious. Androecia on leading shoots or elongate, indeterminate, intercalary branches, the ventral- and lateral-intercalary branches of about equal frequency, rarely and sporadically on terminal branches, the androecia subfolious to subspicate; bracts slightly to moderately smaller than leaves, often similar in shape to vegetative leaves except for development of a lobule, the bracts suberect to spreading, strongly dorsally assurgent, loosely appressed to bract immediately above, the saccate portion crenulate in profile and fused toward base with opposite bract, the apex bilobed to undivided and truncate, the ventral margin entire; lobule margin involute, crenate-denticulate and with copious slime papillae; antheridia solitary, the stalk uniseriate but distally locally biseriate. Gynoecia (only immature seen) nearly always on intercalary branches, mostly ventral, sporadically lateral, the intercalary branches short and without normal leaves, rarely moderately long, the gynoecia sporadically on main shoot but never on terminal branches. Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free from one another, concave to convex, ovate; apices retuse-bidentate to short bifid, the lobes apiculate to ± acuminate, plane, entire; lamina margins plane to somewhat reflexed, the margins entire. Bracteoles of innermost series somewhat smaller than bracts, free or narrowly connate on 1 side, slightly convex, ovate to obovate; apices short bifid, the lobes medium acute to apiculate; lamina margins entire. Perianth ± sharply trigonous throughout, elliptic to obovate, not narrowing toward the shallowly 3-lobed mouth; lobes obscurely bifid, the segments small, triangular to subacuminate, entire, the lobes otherwise with a few small teeth below level of segments; keels rather sharp, with keelar wings common but not on all 3 keels, rather high, with a few teeth.

Sporophyte not seen.

DIFFERENTIATION—I have studied a suite of Allison collections determined as *Lophocolea novaezeelandiae* that have bifid leaves and abundant gemmae. This may be the plant that Hodgson (1953, p. 332) referred to under *L. novaezeelandiae* as having "remote little leaves with uneven margins and apices" and with "margins often uneven to erose." I have removed this element from *C. novaezeelandiae*

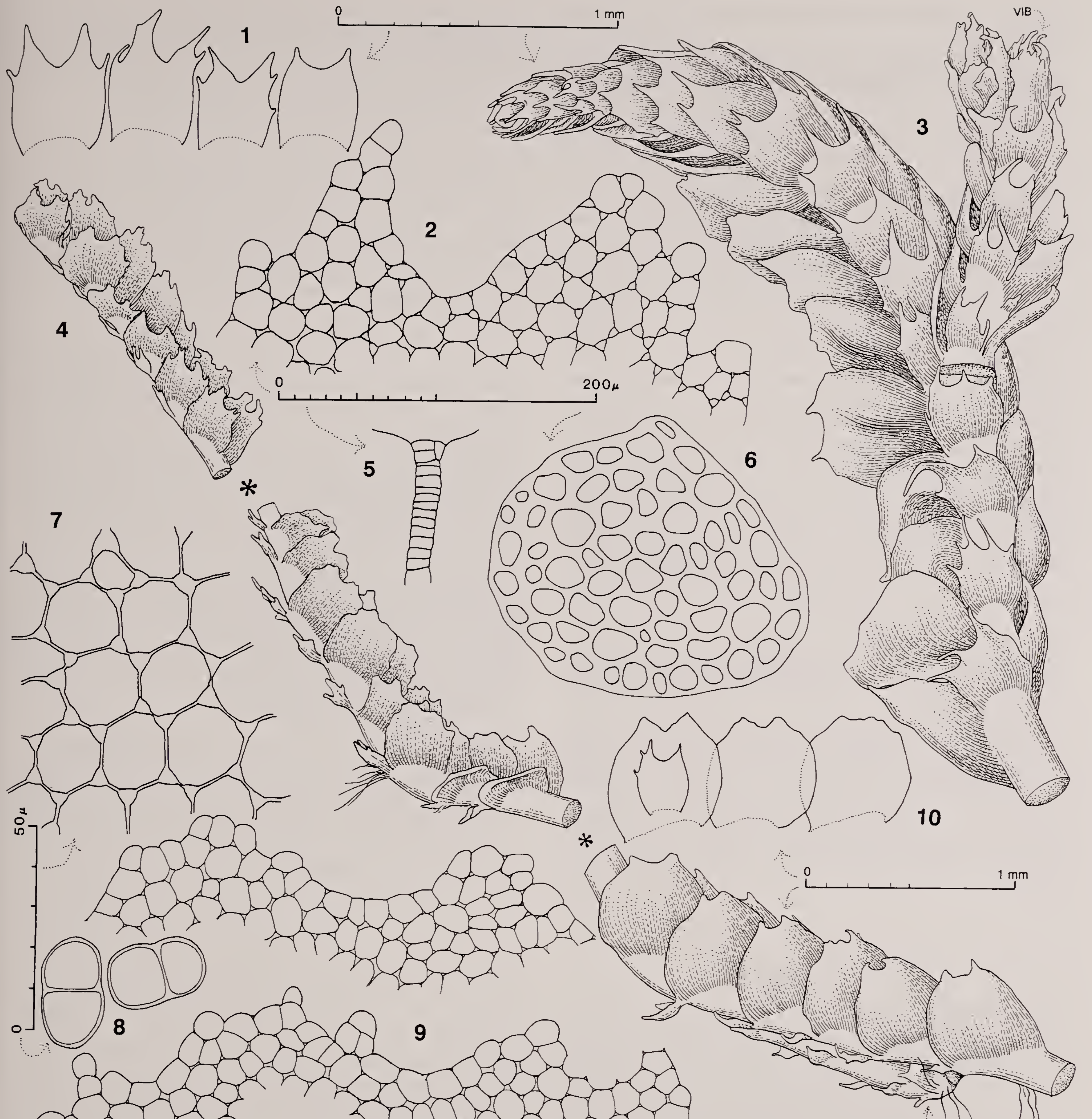

FIG. 27. *Chiloscyphus erosus* J. J. Engel. **1.** Underleaves. **2.** Distal sector of leaf from near shoot apex. **3.** Leading shoot with a ventral-intercalary branch, which in turn produces a ventral-intercalary branch (= VIB). **4.** Leading shoot with a ventral-intercalary branch; note irregularity of leaf apices (lateral view). **5.** Antheridium. **6.** Stem, cross section. **7.** Median leaf cells. **8.** Two gemmae. **9.** Distal sectors of 2 leaves from median sector of shoot. **10.** Leaves and within at left an underleaf. (**1–4, 6, 7, 9, 10,** from holotype; **5,** from *Allison 3563*, New Zealand, North Is., South Auckland Prov., Kaingaroa Plains; **8,** from *Allison 3570*, New Zealand, North Is., South Auckland Prov., Plateau E of Waiotapu Valley.)

because it considerably distends that species by having 1) underleaves often convex (ventral view), 2) underleaves often bifid to 0.9, 3) distinctly thick-walled stem cells (Fig. 27: 6), and 4) shoots that often become flagelliform. *Chiloscyphus erosus* is superficially similar to *C. novaezeelandiae* var. *grandistipulus* of sect. *Novarum-zeelandiarum*, and care should be exercised in separation of these two taxa. Besides being differentiated by the above characters, *C. erosus* has gemmae abundant, whereas var. *grandistipulus* only sporadically produces them.

The species is most closely allied with *C. perpusillus*. Characters in the key to sect. *Lophocolea* will distinguish the species.

Note—The erose condition is best developed on sterile and gynoecial shoots and to a lesser extent on androecium-bearing shoots.

Distribution and Ecology—Endemic to New Zealand, this species is known only from three stations on South Is. (Otago and Nelson Prov. only, 15–1580 m) and several on North Is. (South Auckland and Hawke's Bay Prov. only, 490–550 m). It occurs on moist, shaded rock and banks. At the Mt. Arthur site, the species occurred in a sinkhole of 3–4 m deep within subalpine scrub and grassy vegetation. It was found at the bottom of the depression in a cool and damp niche under moderately heavy shade among rock and vegetation consisting of *Acaena profundincisa*, *A. fissistipula*, *Ranunculus insignis*, *Celmisia traversii*, *Geum*, *Geranium*, and *Craspedia* (Elizabeth Brown, in litt.).

Specimens Seen—**NEW ZEALAND. SOUTH ISLAND. OTAGO:** Dunedin, Abbott's Hill, *Simpson s.n.* (CHR). **NELSON:** Cape Foulwind, W of Westport, ca. 15 m, *Child H 3599* as *L. amplectens* (F); Mt. Arthur, ca. 1580 m, *Brown 88/36d* (AK). **NORTH ISLAND. HAWKE'S BAY:** Wairoa, "Kiwi," *Allison H 3567* as *L. novaezeelandiae* (CHR). **SOUTH AUCKLAND:** Kaingaroa Plains, near Rotorua, *Allison H 3563* as *L. novaezeelandiae*–c. per. + ♂ (CHR); plateau E of Waiotapu Valley, S of Rotorua, ca. 490–550 m, *Allison H 3394*–c. ♂, *H 3570*, both as *L. novaezeelandiae* (CHR).

Sect. *Novarum-zeelandiarum* J. J. Engel

Chiloscyphus sect. *Novarum-zeelandiarum* J. J. Engel, Novon 9: 22. 1999, "*Novae-zeelandii*." Type: *Jungermannia novaezeelandiae* Lehm. & Lindenb.

Branching terminal-lateral and lateral-intercalary or strictly lateral-intercalary; ventral-intercalary branches lacking. Leaves fundamentally undivided, polymorphic: undivided and rounded to retuse to 1-lobed to shallowly bilobed, at times all or a combination of these variants on 1 shoot, the lobes, when present, often blunt to rounded (leaves consistently bifid in *C. novaezeelandiae* var. *grandistipulus* or consistently undivided in *C. novaezeelandiae* var. *meridionalis*); margins entire or armed with 1 or more teeth (gemmiparous shoots of *C. novaezeelandiae*). Leaf cells with trigones medium and straight sided to large to knot-like. Underleaves bifid to 0.4–0.85; lamina margins 1–3-dentate-ciliate.

Asexual reproduction by gemmae (*C. novaezeelandiae*) or lacking.

Plants dioecious. Androecia often forming elongate spikes; bracts slightly to distinctly smaller than leaves. Gynoecia on main shoots or long, leafy, lateral-intercalary branches, never on short intercalary branches that lack leaves, never on terminal branches. Capsule wall inner layer with continuous sheets of pigmented thickening on vertical radial walls. Spore:elater diameter ratio 1.1–2:1.

Section *Novarum-zeelandiarum* is strictly Australasian, with the exception of one species in New Guinea (see below). It is closely related to sect. *Heterophyllae* (R. M. Schust.) J. J. Engel & R. M. Schust. (Engel and Schuster, 1985), which includes only the holarctic *C. profundus* (Nees) J. J. Engel & R. M. Schust. (= *L. heterophylla* (Schrad.) Dumort.) and *C. minor* (Nees) J. J. Engel & R. M. Schust., but differs from that section in being uniformly dioecious and in having androecia often forming elongate spikes with bracts that are slightly to markedly smaller than the leaves.

Gynoecia in the *Heterophyllae* may occur on abbreviated lateral-intercalary branches lacking vegetative leaves (as in *C. profundus* subsp. *cladogynus* (R. M. Schust.) J. J. Engel (Engel, 1998) ≡ *Lophocolea heterophylla* subsp. *cladogyna* R. M. Schust., Hep. Anthoc. N. Amer. 4: 223. 1980); that condition never occurs in the *Novarum-zeelandiarum*.

Also apparently belonging here is:

Chiloscyphus morobeanus (Piippo) J. J. Engel, **comb. nov.**

Lophocolea morobeana Piippo, Acta Bot. Fennica 131: 160, *fig. 19i–p.* 1985. Holotype: Papua New Guinea, Morobe Prov., E of Wantoap River, ca. 8 km NNW of Wantoat, 1500–1700 m, *Norris 60507* (see Piippo, 1985).

Sect. *Novarum-zeelandiarum*

Key to Taxa of Sect. *Novarum-zeelandiarum*

1. Leaf apices highly variable: broadly rounded to truncate to retuse to (often) 1- or 2-lobed; oil-bodies (where known) rather finely papillose. Leaf apices normally complete and not erose margined 2
  2. Underleaf disk plane or convex (ventral view); gemmae lacking. New Zealand 3
    3. Plants small, 0.5–1 mm wide, often pale brown (at least in herb.); terminal branching prevalent; leaves bordered by 1 (locally 2) rows of larger cells; underleaves 0.9–1.8× stem width; gynoecia always on main shoot; spores 13.5–15.4 µm, spore:elater diameter ratio 1.6–2.1:1; plants of calcareous substrates . . . . *C. calcareus* (p. 87)
    3. Plants larger, to 2 mm wide, pale green; terminal branching lacking; leaves without a border; underleaves 1.6–2.8× stem width; gynoecia often on lateral-intercalary branches; spores 10.1–11.5 µm, spore:elater diameter ratio 1.1–1.4:1; plants of noncalcareous substrates. Oil-bodies 3–6 per cell . . . . *C. hattorii* (p. 84)
  2. Underleaf disc all or mostly concave (ventral view); gemmae occasionally present. Oil-bodies 2(3) per cell. New Zealand, Tasmania, SE Australia . . . . *C. novaezeelandiae* var. *novaezeelandiae* (p. 80)
1. Leaf apices slightly variable: either all or nearly all bilobed or all or nearly all undivided (and if retuse, then never developing lobes); oil-bodies (where known) coarsely botryoidal and with segments well-defined 4
  4. Leaves broadly rounded to truncate, sporadically retuse but never developing lobes, the plants appearing like phases of *C. austrigenus* or *C. semiteres* in dorsal view; median leaf cells larger, 22–35 µm wide × 31–40 µm long . . . . *C. novaezeelandiae* var. *meridionalis* (p. 82)
  4. Leaves all or nearly all bilobed; median leaf cells smaller, 14–26 µm wide × 16–29 µm long 5
    5. Underleaves consistently concave (ventral view); underleaf lamina margins commonly 1–3(4)-dentate; gemmae sporadic . . . . *C. novaezeelandiae* var. *grandistipulus* (p. 83)

5. Underleaves plane to convex (ventral view), isolated exceptions aside; underleaf lamina margins all or mostly on each side with a dentiform to laciniiform process; gemmae abundant 6
    6. Leaf apex form ± consistent throughout shoot (exc. at shoot tips, where lobes are complete): lobes with uniseriate row of cells caducous, the mature leaves with lobes terminating in 2(3) laterally juxtaposed cells that frequently possess secondary septa; leaves without accessory lobes at apex, never 4-lobed, never with complete loss of lobes; vegetative branches mostly of *Frullania* type, occasionally lateral intercalary, never ventral intercalary; shoots distally plane, neither cernuous nor flagelliform; stems narrow for plant size; ♀ never on ventral-intercalary branches; stem cells thin walled. Tasmania (rather common); very rare in New Zealand (Auckland Is.; Campbell Is.; South Is.); very rare in Australia (NSW) . . . . [*C. perpusillus*] (p. 67)
    6. Leaf apex (gemmiparous leaves) becoming abnormal and progressively more erose, with continued gemmae formation the lobes disappearing altogether (the leaf apex then ± broadly rounded); leaves often with 1–2 accessory lobes at apex lending a ragged appearance; vegetative branches all or mostly intercalary (both lateral and ventral); shoots distally often cernuous, sometimes becoming flagelliform; stems thick and fleshy for plant size; ♀ often on ventral-intercalary branches; stem cells thick walled. Plants to 0.8 mm wide. New Zealand. . . . . [*C. erosus*] (p. 72)

Chiloscyphus novaezeelandiae (Lehm. & Lindenb.) J. J. Engel & R. M. Schust.

Jungermannia novaezeelandiae Lehm. & Lindenb. *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. 6: 33. 1834. *Lophocolea novaezeelandiae* (Lehm. & Lindenb.) Nees *in* Gottsche, Lindenb. & Nees, Syn. Hep. 168. 1845. *Chiloscyphus novaezeelandiae* (Lehm. & Lindenb.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 420. 1985 (1984). Type: New Zealand, South Is., Dusky Bay, *sin. coll.* [*Menzies*](BM!, G!, S![2], ex hb. Hooker–c. per.).

Plants flexuous, ascending to erect, light green, nitid when dry; shoots to 2.2 mm wide. Branches common, of *Frullania*- and lateral-intercalary types, the two types of ± equal frequency (exc. var. *grandistipulus* where often predominantly intercalary), the lateral-intercalary branches usually originating immediately above leaf–underleaf connation. Stem rather narrow for plant size, 11–12 cells high, the cortex rather poorly differentiated, in 1–2 layers of rather thick-walled cells that average slightly smaller than the somewhat thick-walled medullary cells. Rhizoids in tight fascicles from stem at immediate base of underleaves. Leaves alternate, strongly dorsally assurgent at least in basal sector and often so throughout, widely spreading, loosely imbricate, free dorsally, the orientation strongly succubous, the insertion at ventral end not to slightly recurved to more strongly so and then weakly J-shaped, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves convex, subsymmetric, ranging from ovate and 1–1.3× longer than wide to wide ovate to suborbicular to suboblate and then 1–1.3× wider than long; apex often broadly and gently deflexed, plane or crenulate, often polymorphic (var. *novaezeelandiae*) and then undivided and rounded (mostly broadly so, occasionally tapering and narrowly so) to truncate to retuse to 1-lobed to (often) shallowly bilobed, the apex in some populations nearly exclusively undivided and with little variability (var. *meridionalis*), the apex in other populations nearly exclusively shallowly bilobed (var. *grandistipulus*); lobe(s) (when present) also polymorphic, grading from median to wide acute to ± apiculate to acuminate (often all variants on a single shoot), the lobe margins entire; dorsal margin broadly and gently curved, plane or sporadically deflexed, entire; ventral margin broadly rounded but somewhat more strongly arched than the dorsal, plane or at times slightly deflexed (particularly in basal sector), entire. Leaf apex (including lobes, when present), and dorsal and ventral margins often armed with small, few-celled teeth on gemmiparous shoots. Leaf cells with walls thin, trigones usually medium and straight sided to large and bulging, occasionally small and concave-side, subapical leaf cells 17–25 μm wide and long, median leaf cells 16–25 μm wide × (17)19–30 μm long to 22–35 μm wide × 31–40 μm long, median basal cells 19–29 μm wide × 29–40 μm long. Oil-bodies in all leaf cells, rather large for cell size, hyaline and glistening, 2(3) to 2–3 per leaf cell, rather finely papillose to coarsely botryoidal and with well-defined segmentation, ovoid to elliptic (and with the ends often narrowly rounded to truncate), grading to fusiform, less often subglobose, 3.3–5.2 × 7.2–9.8 μm to 4.6 × 9.8–11.7 μm, the subglobose ones 4.6 × 5.9 to 5.2 × 6.5 μm. Underleaves much smaller than leaves, 1.4–3.3(4.8)× stem width, narrowly connate on 1 or, rarely, 2 sides, occasionally free on both sides (but underleaf and leaf insertions on 1 side closely juxtaposed), the insertion often asymmetric, crescentic to more often inverted U-shaped, the underleaves moderately spreading to ± subsquarrose, distant to approximate, typically with at least the lamina or at times the entire underleaf slightly to distinctly concave (ventral view), ovate to elliptic-subrectangular, bifid to (0.2)0.4–0.6(0.8) by a U- to broadly V-shaped to lunate sinus; lobes ± parallel to moderately diverging, medium acute to acuminate to subcaudate, the lobe margins entire, rarely with a cilium; lamina margins commonly recurved, 1–3(4)-dentate, occasionally with 1 of the processes laciniiform, sometimes entire. Underleaves on both young and mature gynoecial shoots frequently are wide spread to squarrose and more deeply concave than those on sterile shoots.

Asexual reproduction occasional, by gemmae produced at leaf apices, the leaf tips then often becoming erose, the gemmae often produced at tips of filamentous processes that may be accompanied by a rhizoid at its base; gemmae 2-celled, 20–23 μm × 26–31 μm. ?Asexual reproduction also by caducous teeth and subtending rhizoid of leaf margins.

Plants dioecious. Androecia on main shoot or leading, indeterminate, *Frullania* or lateral-intercalary branches, initially terminal but eventually become intercalary, the ♂ branches sometimes appearing to cease growth (and occasionally lack vegetative leaves) but at other times proliferate vegetatively distally (the androecium then basal on a branch), the androecia subspicate to subfoliose; bracts somewhat to distinctly smaller than leaves, hardly more erect or dorsally assurgent than leaves, loosely to rather tightly appressed to bract immediately above, the saccate portion crenulate in profile and fused toward base with opposite bract, the bracts ventricose in basal portion, the distal portion reflexed and weakly to distinctly convex to subcanaliculate and with a form basically similar to leaves, the apex less variable than in leaves and grading from (often) broadly rounded to truncate to (less

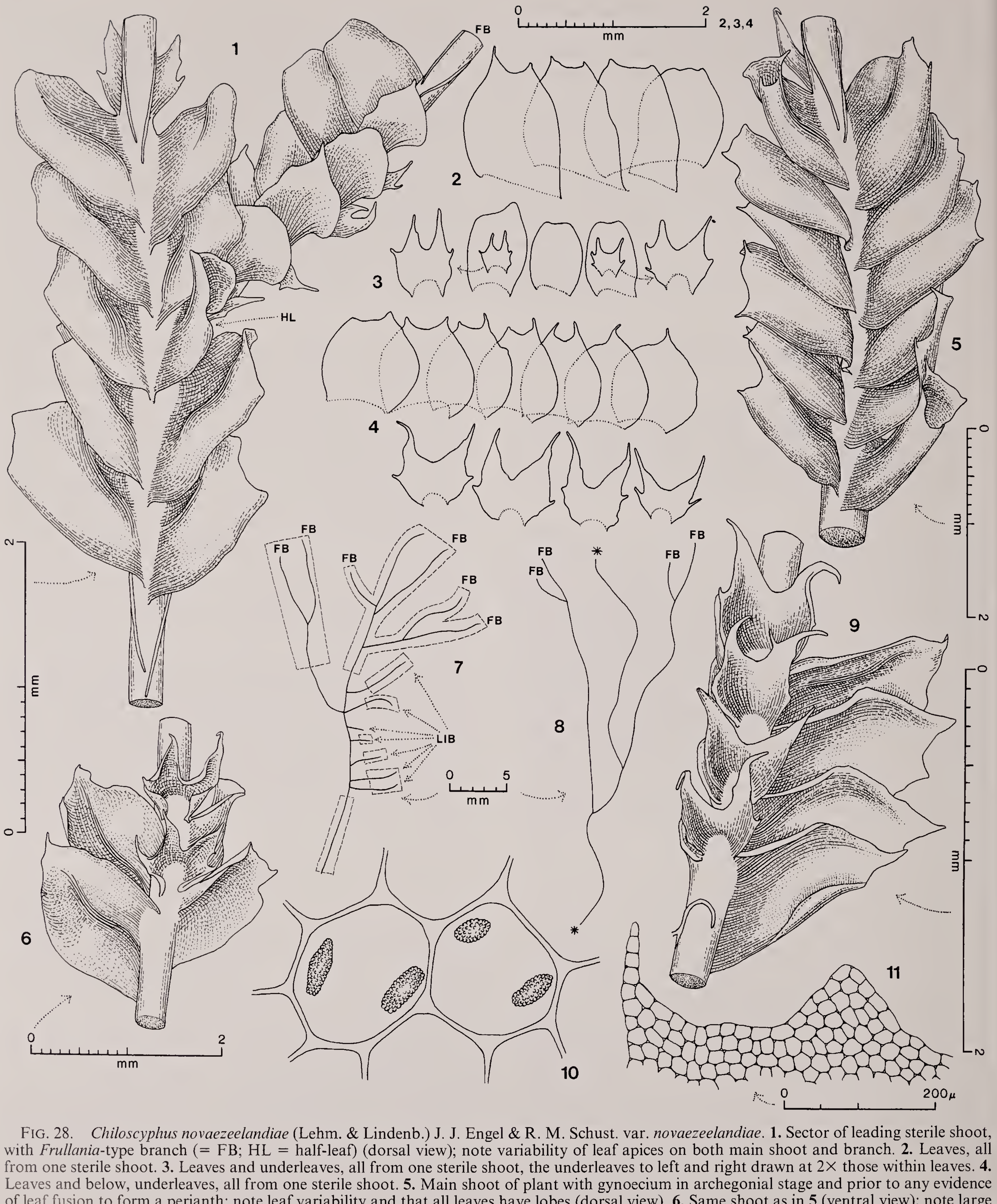

FIG. 28. *Chiloscyphus novaezeelandiae* (Lehm. & Lindenb.) J. J. Engel & R. M. Schust. var. *novaezeelandiae*. **1.** Sector of leading sterile shoot, with *Frullania*-type branch (= FB; HL = half-leaf) (dorsal view); note variability of leaf apices on both main shoot and branch. **2.** Leaves, all from one sterile shoot. **3.** Leaves and underleaves, all from one sterile shoot, the underleaves to left and right drawn at 2× those within leaves. **4.** Leaves and below, underleaves, all from one sterile shoot. **5.** Main shoot of plant with gynoecium in archegonial stage and prior to any evidence of leaf fusion to form a perianth; note leaf variability and that all leaves have lobes (dorsal view). **6.** Same shoot as in **5** (ventral view); note large underleaves and lobed leaves. **7.** Cladograph showing extraordinary production of androecia on main shoot and all branches (FB = *Frullania*-type branch; LIB = lateral-intercalary branch; stippled lines indicate boundaries of sectors with male bracts possessing well-developed lobules), even the half leaves associated with *Frullania*-type branches commonly possess a lobule. **8.** Cladograph, all branches of *Frullania* type (= FB; * = extremities of main shoot). **9.** Sector of leading sterile shoot (ventral-lateral view); note the variability of leaf apex, of underleaf connation with some completely free, while others (shown at extreme base of shoot by insertion scar only) connate on one side, and of underleaf segment armature. **10.** Oil-bodies (X 000). **11.** Leaf apex. (**1, 2, 8, 10,** from *Engel 20152*, Tasmania, Great Western Tiers, Walls of Jerusalem Natl. Park; **3,**

often) medium acute and then often apiculate, the ventral margin entire; lobule margin inflexed to involute, irregularly crenate, occasionally with a small lobe, otherwise with numerous slime papillae; antheridia 1 per bract, the stalk uniseriate. Gynoecia on main shoot and leading lateral-intercalary branches; subfloral innovations occasional. Bracts of innermost series much larger than leaves, erect and ensheathing perianth base, free from one another, weakly to strongly concave-canaliculate, especially distally, ovate to ovate-elliptic; apices retuse (?suboptimal) to bifid to 0.15–0.3, the lobes narrow to medium acute, at times apiculate to subacuminate, entire; lamina margins plane to distinctly reflexed, the ventral somewhat more arched than the dorsal, the margins entire or with 1–2 teeth. Bracteoles of innermost series subequal to bracts in size and form, free or narrowly connate on 1 side, distinctly concave, ovate to ± orbicular; apices 0.15–0.2 bifid, the lobes medium acute to acuminate, entire; lamina margins entire or with a tooth or small lacinium. Perianth longly exserted beyond bracts, sharply trigonous throughout, narrowly oblong to narrowly elliptic, not or slightly narrowing toward the wide, rather deeply 3-lobed mouth; lobes rather deeply bifid, the segments acuminate to subcaudate, usually entire but at times with 1–2 teeth, the lobes otherwise with a few accessory teeth and at times 1 or more laciniae; keels sharp, with keelar wings common, to ca. 10 cells high and often with several teeth. Calyptra small, ca. 0.6 perianth length at maturity.

Seta 7–8 cells in diam., with 21 rows of outer thick-walled cells surrounding an inner core of scattered cells averaging about the same size as the outer cells, the inner cells thin walled and with corners thickened as in knot-like trigones. Capsule elliptic, 945 × 630 µm to 980 × 735 µm, the wall 34–37 µm thick, of 4–5 layers, the outer layer of cells equal to thickness of all of interior strata; outer layer of cells subquadrate to short rectangular, the radial walls with magenta thickenings that are nodular but only sporadically and feebly spine-like, the thickenings mostly on longitudinal walls, sporadically and often feebly represented on transverse walls; innermost layer of cells long and often narrowly rectangular, the vertical radial walls with continuous sheets of red-brown wall material, with semiannular bands red brown, common, narrow, often nonpigmented in median portion, only a few bands per cell complete, the bands sporadically forked, the radial walls with nodular to spine-like thickenings rather common.

Spores 13.9–16.8 µm, yellow brown, very thin, with faint, dense, low, defined, close papillae and numerous short vermiculate markings, spore:elater diameter ratio 1.4–2:1. Elaters tortuous, 8.2–9.6 µm wide, the spirals 1.9–2.4 µm wide, closely wound.

VARIATION—*Chiloscyphus novaezeelandiae* has striking variability, and extremes of phenotypic expressions appear very different. Furthermore, the species is common in both New Zealand and Tasmania, and therefore the student interested in learning at least the common Australasian hepatics should attempt to grasp this variability. Leaf apices commonly vary from broadly rounded to retuse to 1- to 2-lobed, with all variants frequently on a single shoot (Fig. 28: 4). Underleaves also are highly variable, and may differ considerably even on a single shoot (see discussion of *Schuster 60178* below).

Gemmiparous shoots appear quite different from those that are free of gemmae. Gemmae are produced at the leaf apices, and may be best observed at or near shoot tips. Leaves of the median and basal sectors of gemmiparous shoots often appear erose. Furthermore, leaves bearing gemmae often also have a few to several small, few-celled teeth at the apex (Fig. 29: 10, 11) (the teeth may occur on lobes of lobe-bearing phases) as well as on dorsal and ventral margins (Fig. 29: 5). It is unclear whether such teeth also may cut off gemmae, or if perhaps the tooth together with the subtending rhizoid (Fig. 29: 5, 10), which is also often present, are caducous and act as a propagule unit. Gemmae-free populations have leaf apices and margins uniformly free of accessory small teeth.

Underleaf concavity is normally expressed and is a valuable and reliable diagnostic feature used in the key. However, submerged plants, such as *Engel 19107*, may offer problems because underleaves often are plane. Such plants should be carefully studied, especially to establish even sporadic presence of concave underleaves. Feebly to demonstrably concave underleaves may be found particularly on distal sectors of shoots. Presumably the typical underleaf form is somewhat altered with submersion, and concavity is suboptimally expressed. In work with such populations, ecology is particularly useful in identification in that the species normally occurs on rocks and boulders of stream beds and banks.

Rare and sporadic populations have predominantly plane to even convex underleaves. When working with such specimens, careful search should be made for presence of concave underleaves as well as secondary cell wall divisions, which are an indicator of gemmae formation.

DIFFERENTIATION—Despite the marked variability exhibited by *C. novaezeelandiae*, the following ensemble of features will distinguish the species: 1) leaves dorsally assurgent at least in the basal sector (Fig. 28: 9), the entire leaf commonly strongly so (Fig. 29: 4); 2) leaf apices often polymorphic (Fig. 28: 2, 4) and basically convex (Fig. 28: 1); 3) underleaves concave, at times markedly so (Fig. 28: 6, 9); 4) underleaves bifid to 0.4–0.6 or more, the lobes well developed (Fig. 28: 3, 4); and 5) *Frullania*- and lateral-intercalary–type branching both common (Figs. 28: 1; 29: 4).

Chiloscyphus novaezeelandiae shows some relationships to *C. austrigenus* subsp. *okaritanus*, especially mod. *retusifolia-undulatifolia* of that taxon, and certain phases of the former species are likely to offer confusion. Particular care should be taken here because the two species may occupy similar niches (on rock associated with running water) and may occur at the same locality (for example, Lake Marion Track, Fiordland Natl. Park, leg. *Schuster*). The relationship between the two taxa occurs through *C. novaezeelandiae* var. *meridionalis* (cf. below), and phases with subhorizontal leaf orientation appear strikingly like *C. austrigenus* var. *okaritanus*, especially in dorsal aspect (compare Figs. 28: 1 and 2: 2). Furthermore, some populations of both phases have leaves that taper to a narrowly rounded summit. A shoot from *Schuster 60178* is

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←

from *Engel 14692*, Tasmania, Gordon River; **4, 9, 11,** from *Schuster 60178*, New Zealand, South Is., ca. 0.5–0.6 mi. from front of Fox Glacier; **5–7,** from *Engel 18753*, New Zealand, South Is., Fiordland Natl. Park, East Branch of Eglinton River.)

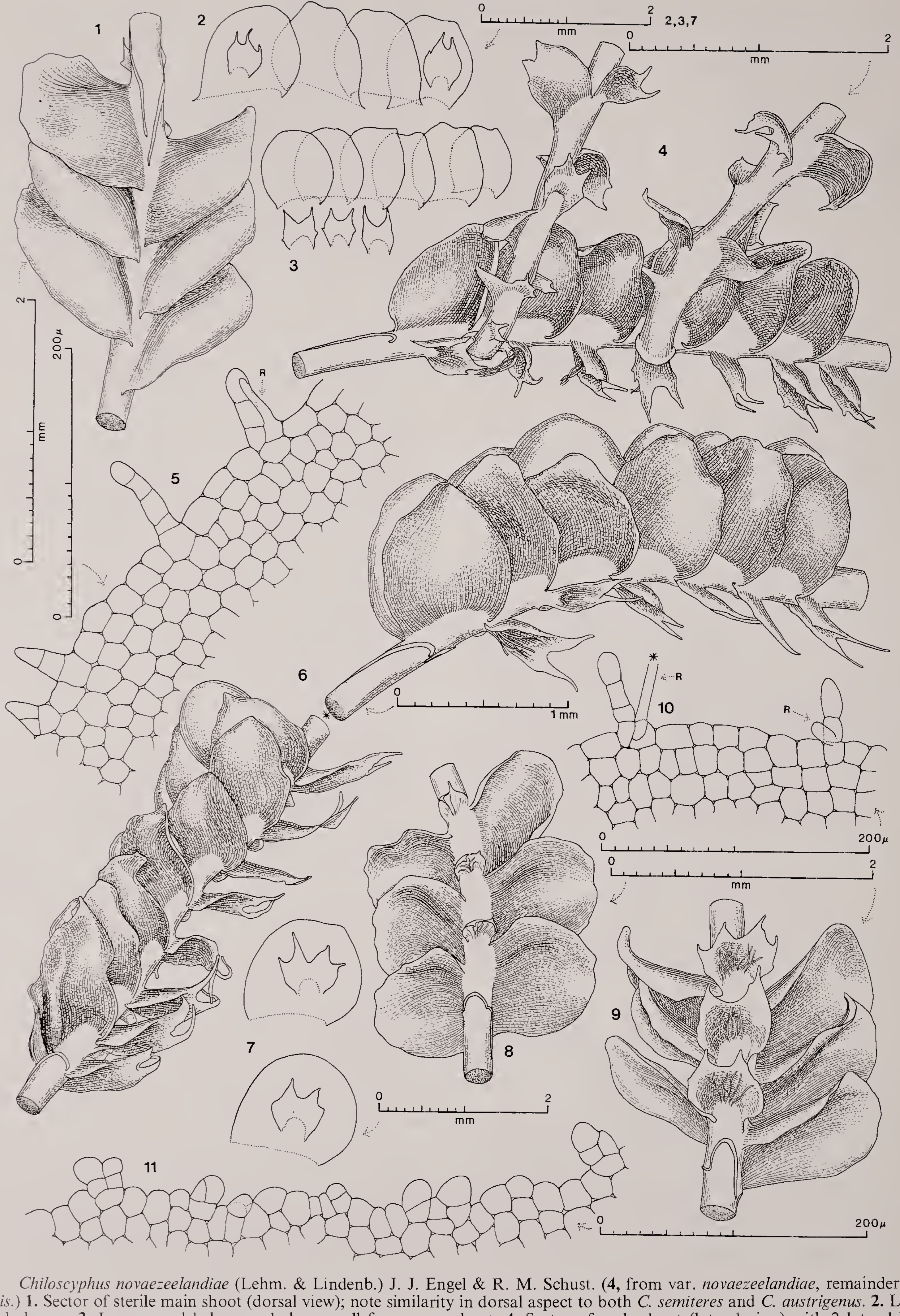

FIG. 29. *Chiloscyphus novaezeelandiae* (Lehm. & Lindenb.) J. J. Engel & R. M. Schust. (**4,** from var. *novaezeelandiae*, remainder from var. *meridionalis*.) **1.** Sector of sterile main shoot (dorsal view); note similarity in dorsal aspect to both *C. semiteres* and *C. austrigenus*. **2.** Leaves, and within, underleaves. **3.** Leaves, and below, underleaves, all from same shoot. **4.** Sector of male shoot (lateral view) with 2 lateral-intercalary branches, the basal one (sterile) originating from ventral part of stem midway between 2 underleaves, the distal one (androecial) from ventral-lateral part of stem in ventral-lateral extremity of underleaf axil. Note large, strongly concave underleaves, minimal variability of leaf apices, and that all leaves have the insertion strongly recurved at ventral end. **5.** Sector of dorsal margin of leaf showing filamentous teeth (which may produce gemmae) and rhizoid (= r) (the cells from apex of same leaf are shown in **11**). **6.** Two sectors (separated by an asterisk) of same male shoot—at lower left, the

TABLE 8. Comparison between *Chiloscyphus novaezeelandiae* var. *meridionalis* and *C. austrigenus* mod. *retusifolia-undulatifolia*.

Character	***C. novaezeelandiae* var. *meridionalis***	***C. austrigenus* mod. *retusifolia-undulatifolia***
Underleaf concavity	distinctly concave	mostly plane to slightly concave
Underleaf sinus	lunate	narrowly rounded, sporadically sharply angular
Underleaf margins	1–3-dentate	at most with 1 tooth
Underleaf sinus depth	often divided to more than 0.4	divided to 0.3 or less
Bracteole apex	short bifid	bidentate to retuse-bidentate
Gemmae	potentially present	lacking

particularly revealing because it illustrates the wide spectrum of variation characteristic of *C. novaezeelandiae*, with one sector "mimicking" subsp. *okaritanus*, and the other (upper) sector very different from it. The basal half of the shoot has underleaves ovate to ± rotund, 2.3–4.8× the stem width, bifid to ca. 0.2–0.4 and slightly concave to plane to slightly convex. Such underleaves grade to quite different ones in the distal sector, which are ovate-rectangular, 1.8–2× the stem width, bifid to ca. 0.6–0.8 and slightly concave.

Although the two species have phases that approach one another, their respective patterns of variation are in quite different directions. For example, subsp. *okaritanus* mod. *retusifolia-undulatifolia* may have underleaves divided to 0.3, but this represents the extreme sinus depth. *Chiloscyphus novaezeelandiae*, on the other hand, normally has underleaves divided minimally to 0.4; in no case do we find undivided underleaves or those with a retuse-bidentate apex, both of which are normal for subsp. *okaritanus*. The two phases may be distinguished in Table 8.

Plants of *C. novaezeelandiae* bring to mind those of *C. semiteres* of sect. *Semiteres*, with which it shares numerous vegetative features. For example, the two are similar in 1) leaves alternate, dorsally assurgent (at least basally), overall convex, and entire margined; 2) cell size (the cells of *C. novaezeelandiae* are somewhat smaller but overlap the range of *C. semiteres*); 3) trigone size; and 4) underleaves asymmetrically inserted, wider than the stem, (often) narrowly connate on 1 side, and distinctly bifid. Few vegetative characters are absolute in separating the species, but underleaf form is the most reliable feature—concave in *C. novaezeelandiae* and plane to convex in *C. semiteres*. Other vegetative characters are useful, but only for some plants. For example, underleaves of *C. semiteres* have a prominent lacinium on each side of the lamina, while those of *C. novaezeelandiae* are usually dentate, and only occasionally do we find a small lacinium. Leaves of *C. semiteres* are rounded to truncate at the summit, while the polymorphic apices of *C. novaezeelandiae* var. *novaezeelandiae* are very distinct. Leaf apices of var. *meridionalis*, however, are more like those of *C. semiteres*. The isolation of these species, and placement into separate sections, is based upon features of the gynoecial apparatus and sporophyte (see key characters, p. 11).

Suboptimal plants of *Chiloscyphus villosus* have notably variable leaf apices and otherwise have a superficial resemblance to *C. novaezeelandiae*. Leaf surface teeth in these variants are at times very difficult to detect, and such plants will key to *C. novaezeelandiae*. Care should be exercised in search of surface teeth, which will immediately place plants among the hispid species. For notes on suboptimal *C. villosus*, see p. 191.

Plants of *Stolonivector fiordlandiae* have a superficial resemblance to *C. novaezeelandiae*, and confusion is possible, particularly in the field. *Stolonivector fiordlandiae* may be immediately distinguished by the convex underleaves and the erect-arching shoots that are often ultimately cernuous and frequently become flagelliform (see Engel 1991a).

NOTES—1) Lateral-intercalary branches commonly originate in the "axil" of the connation tissue attaching leaf and underleaf, or if on the side opposite leaf–underleaf connation (i.e., the side of the shoot with no leaf–underleaf attachment), then from near the ventral end of the leaf axil. Such positions, however, are not constant, and one finds gradations toward a ventral-lateral or even a ventral site. Lateral branches grade to those that may be ventral/ventral-lateral and near or in the axil of half of the underleaf (Fig. 29: 4). The latter position grades to one in which the branch issues from the ventral side of the stem adjacent to the ventral base of the leaf but midway between two underleaves (Fig. 29: 4). Branches issuing from the ventral side of the stem are not in the median sector of an underleaf axil, and therefore confusion with true ventral-intercalary branches is avoided.

2) *Chiloscyphus novaezeelandiae*, at least at times, is sexually dimorphic. For example, androecium-bearing plants of *Engel 18753* have vegetative leaves with apices normally nonvariable and broadly rounded (Fig. 29: 4). Leaves on such male shoots only exceptionally are feebly 1- or 2-lobed or narrowed to a medium-acute tip. Gynoecial shoots, on the other hand, normally have leaf apices 1- or 2-lobed, and only exceptional leaves are unlobed. These differences may be observed not only on shoots with young perianths, but on those with gynoecia in the archegonium and pre–perianth formation stages (Fig. 28: 5, 6). *Engel 18909* also illustrates this dimorphism. This collection consists of both sterile and androecial plants. Androecial shoots have bracts and sterile leaves minimally variable and with apices basically broadly

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zone of male bracts (5 ♂ bracts shown, the 2 distal leaves are without pockets), at upper right, sterile leaves (lateral view). Note minimum variability of leaf apices of sterile leaves and the extent of insertion recurvature at ventral base. **7.** Leaves, and within, underleaves. **8.** Sector of sterile shoot representing a common phase of the species (ventral view); note underleaves may be free or very narrowly connate on 1 side. **9.** Sector of sterile, leading lateral-intercalary branch, ventral view. **10.** Sector of leaf apex; note gemmae and rhizoids (= r), the one at left extending 180 µm, that at right in young stage. **11.** Sector of leaf apex; note filamentous teeth (which may produce gemmae) and crenulation. (**1, 7, 8,** from *Engel 15759*, Tasmania, Leven Gorge; **2,** from *Engel 15958*, Tasmania, Great Western Tiers, near Lake Salome; **3,** from *Engel 18451*, New Zealand, South Is., Arthur's Pass Natl. Park, Bealey River (mixed with var. *grandistipulus*); **4,** from *Engel 18753*, New Zealand, South Is., Fiordland Natl. Park, East Branch of Eglinton River; **5, 9, 11,** from *Engel 14695A*, Tasmania, Gordon River; **6,** from *Schuster 60178*, New Zealand, South Is., 0.5–0.6 mi. from front of Fox Glacier (mixed with var. *novaezeelandiae*); **10,** from *Engel 14698*, Tasmania, Gordon River.)

rounded to truncate to at most (and only occasionally) feebly retuse. Sterile shoots, on the other hand, have leaf apices mostly 1- or 2-lobed. Exceptions to the conservative nature of the androecium may be found in var. *meridionalis* (see below). Here androecial shoots may have sterile leaves broadly rounded at the summit, but have male bracts tapering toward the apex (Fig. 29: 6).

Subspecific Differentiation—The boundaries of three phases of *C. novaezeelandiae* are particularly troublesome. Furthermore, difficulties are enhanced because combinations of two of the three extremes at times, though rarely, occur intermixed. Examples of mixtures of the variable-leaved and constant, undivided-leaved phases of the species are *Schuster 60178* from New Zealand and *Engel 16449* from Tasmania. Intermingling of the two extremes, however, provides an ideal opportunity to assess their nature, and to demonstrate that distinct entities are at hand. These entities are recognized here at the varietal level. Distinction of varieties based on a variable-leaved phase and a constant one with undivided leaves also occurs in another Austral species in the genus: *C. hookeri* J. J. Engel of southern South America (cf. Engel, 1973).

A third phase of the species may be confusing because of a high percentage of leaves with short-bifid apices (Fig. 30: 7–9, 11), and such plants thus may key among plants having bifid leaves. An example is *Schuster 48385*, which was collected on the same day and at the same locality as *Schuster 60178* (South Is., steep, rocky slopes below high cliff in deep glacial valley, ca. 0.5–0.6 mi. from front of Fox Glacier, near township of Fox Glacier), which consists of a mixture of the two varieties of *C. novaezeelandiae* mentioned above. All three varieties thus may be sympatric. Other examples of the bifid-leaved phase are *Engel 18451* (which is intermixed with the constant-leaved phase) and *Engel 18452* (from the same locality and habitat, but with only the bifid-leaved phase present).

The three varieties may be distinguished by the following key.

Key to Varieties of *C. novaezeelandiae*

1. Leaf apices highly variable: broadly rounded to truncate to retuse to (often) 1- or 2-lobed . . . var. *novaezeelandiae*
1. Leaf apices slightly variable: either all or nearly all bilobed or all or nearly all undivided, at most retuse but never developing lobes 2
    2. Leaves broadly rounded to truncate, sporadically retuse but never developing lobes, the plants appearing like phases of *C. austrigenus* or *C. semiteres* in dorsal view; median leaf cells larger, 22–35 μm wide × 31–40 μm long . . . . var. *meridionalis*
    2. Leaves all or nearly all bilobed; median leaf cells smaller, 14–22 μm wide × 16–26 μm long. Oil-bodies coarsely botryoidal and with segments well defined . . . . var. *grandistipulus*

Chiloscyphus novaezeelandiae (Lehm. & Lindenb.) J. J. Engel & R. M. Schust., **var. novaezeelandiae**

Jungermannia grisea Hook. f. & Taylor, London J. Bot. 3: 379. 1844, *syn. fide* Mitten (1854–55). *Lophocolea grisea* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 169. 1845. Type: Auckland Is., Nov. 1840, *Hooker* (BM!–c. ♂, FH!–c. per.).

Lophocolea macrostipula Steph., Bull. Herb. Boissier 6(10): 888. 1906 (= Spec. Hep. 3: 113), *syn. nov. Chiloscyphus macrostipulus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 418. 1985 (1984). Lectotype (*nov.*): Tasmania, Mt. Wellington, St. Crispin's (Well), 24 Jan. 1899, *Weymouth 1509* (G!–c. ♂ + per. + sporo.); isolectotype: (HO!–c. ♂ + per. + sporo.).

Lophocolea sellingii S. W. Arnell, Bot. Not. 115: 314. *f. 2.* 1962, *syn. nov. Chiloscyphus sellingii* (S. W. Arnell) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 422. 1985 (1984). Holotype: Tasmania, near Targa, ca. 15 mi. NE of Launceston, (21 mi. from Launceston along road to Scottscale), St. Patrick's River, 9 Jan. 1949, *Selling s.n.* (S!–c. per. + ♂).

Leaf insertion mostly not or slightly recurved at ventral base, at most "comma-like;" leaves often ovate, longer than wide; leaf apices highly variable: broadly rounded to truncate to retuse to (often) 1- or 2-lobed, the apices often plane and not crenulate, the exposed walls not bulging; leaf cell trigones often large and bulging, even at the leaf base; oil-bodies (1)2(3) per cell, rather finely to coarsely papillose. Underleaf margins normally 1-dentate-laciniate. Gemmae occasional.

Notes on Type Specimens—1) *Jungermannia novaezeelandiae* Lehm. & Lindenb. Material at BM, G, and S consists of a few shoots, some of which bear gynoecia. The plants are flaccid and have leaves with apices varying from broadly rounded to truncate to retuse to (exceptionally) retuse-1 lobed. The concave underleaves (ventral view) are bifid to ca. 0.6–0.7. The bracts are retuse-short bifid to short bifid and the one bracteole examined is orbicular and bifid to ca. 0.2.

2) *Jungermannia grisea* Hook. f. & Taylor Plants are rather small, being 1.2–1.3 mm wide. The leaves have apices varying from rounded to truncate to retuse to 1-lobed and trigones that are bulging to weakly knot-like. The distinctly concave underleaves (ventral view) are ca. 0.6–0.8-fid and have lamina margins entire or, more commonly, with a small tooth. The bract apices are retuse and not "rounded and entire" as stated in the protologue (p. 379). Plate 64 in Taylor and Hooker (1845, fig. 8: 3) clearly shows retuse bracts. The single bracteole studied is short bifid and with entire lamina margins. *Chiloscyphus austrigenus* subsp. *okaritanus* is also present.

3) *Lophocolea macrostipula* Steph. Underleaves are conspicuous, ca. 1.8–2× the stem width, narrowly connate on 1 side, distinctly concave (ventral view), rather wide ovate-elliptic, bifid to ca. 0.3–0.5 by entire-margined lobes, and with lamina margins entire or with a dentiform to sporadically laciniiform process. Leaf apices are variable and broadly rounded to truncate to retuse to short bifid; the lobes, when present, are at most acute and never acuminate. Trigones are conspicuous, medium and straight sided.

Specimens at G and HO bear the same label information except for number. The specimen at G is number 1509, whereas that at HO is 521. The HO specimen has the note "determ'd Stephani (n. 1509)" and is therefore part of the type collection.

4) *Lophocolea sellingii* S. W. Arnell. Plants are in poor condition and were either so on collection or from imperfect drying. Leaf apices are variable: broadly rounded to truncate to 1- or 2-dentate, often on a single shoot. The sinus is at best feebly developed, sometimes merely a suggestion, sometimes lunate. Underleaves are bifid to ca. 0.6–0.7, the disc is concave and on each side has a small to large tooth. The species is said to be autoecious, with androecia "in branches from below the perianth." Arnell also notes that androecia may occur "in separate plants," implying dioecism. I was able to locate a few old, ± decayed gynoecia but found no evidence of physical attachment between androecial and gynoecial plants. Androe-

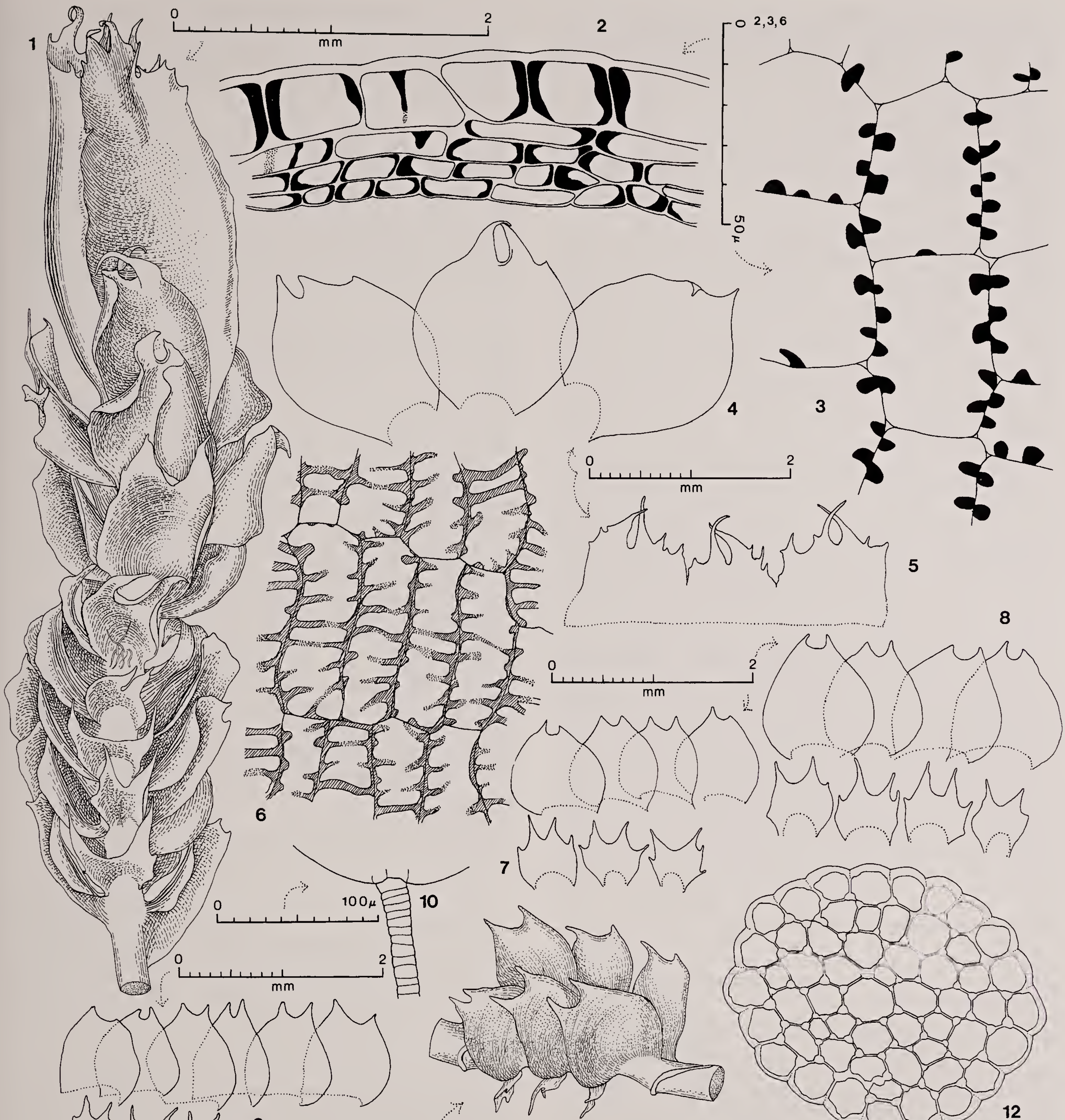

FIG. 30. *Chiloscyphus novaezeelandiae* (Lehm. & Lindenb.) J. J. Engel & R. M. Schust. (**7–9, 11,** from var. *grandistipulus*, remainder from var. *novaezeelandiae*.) **1.** Mature gynoecium; note isophylly of bracts and bracteoles and form of vegetative leaves below; ventral view. **2.** Capsule wall, cross section. **3.** Capsule wall, outer layer. **4.** ♀ Bracts, and in middle, bracteole. **5.** Perianth mouth, ventral lobe in middle. **6.** Capsule wall, inner layer. **7–9.** Leaves, and below, underleaves. **10.** Antheridium. **11.** Sector of main shoot, dorsal-lateral view. **12.** Seta, cross section. (**1, 4, 5,** from *Hatcher 818*, New Zealand, South Is., Fiordland, Martin's Bay; **2, 3, 6, 12,** from *Schuster 60178*, New Zealand, South Is., 0.5–0.6 mi. from front of Fox Glacier; **7,** from *Engel 18479*, New Zealand, South Is., Arthur's Pass Natl. Park, Bealey River; **8,** from *Engel 18452*, New Zealand, South Is., Arthur's Pass Natl. Park, Bealey River; **9, 11,** from *Engel 18451*, New Zealand, South Is., Arthur's Pass Natl. Park, Bealey River; **10,** from *Engel 18753*, New Zealand, South Is., Fiordland Natl. Park, East Branch of Eglinton River.)

cia are common in the specimen and occur in close association with gynoecial shoots. It appears that Arnell confused such close proximity with actual physical attachment of male and female shoots.

Distribution and Ecology—The variety is rather broadly distributed in Australasia, occurring in New Zealand (Stewart Is.; South Is., 30–610 m; North Is., 150–940 m), Australia: Tasmania (sea level–1220 m), Victoria (1400 m), A.C.T. (1550–1680 m), New South Wales (1240–1500 m), and Queensland.

The var. *novaezeelandiae* often is associated with watercourses, occurring commonly on rock or soil of creek, stream and river banks or beds (at times in running water), as well as on rock or cliff faces associated with waterfalls, and then it occurs in the spray zone. It often is present on shaded silt terraces just above normal watercourse levels but within the flood zone. The variety also utilizes other substrates, such as rotting logs beside watercourses. The watercourses are associated with forests of various types throughout the range of the variety. It occasionally occurs in the subalpine zone at the edges of tarns and then the plants are lapped by water.

It also occurs in damp or wet niches of nonwatercourse sites. For example, the variety may be sheltered by sedges in low, rather open, swampy areas. It also may occur on roadside banks or ditches. It may even be present in coastal areas in sheltered niches of steep banks above high tide (Otago Prov., NZ). In subalpine areas it occasionally occurs on rock in swampy heath valleys.

Specimens Seen (selected)—**NEW ZEALAND. STEWART IS.:** Port Pegasus, immediately below Belltopper Falls, North Arm, ca. 5 m, *Engel, von Konrat & Braggins 24124* (F); Port Adventure, *Schuster et al. s.n.* as *L. minor* (CHR). **SOUTH ISLAND. SOUTHLAND:** Bluff Hill, ca. 30–60 m, *Allison H 5165* as *L. austrigenus* (CHR); Fiordland Natl. Park, Dusky Sound, Five Finger Peninsula, *Allan s.n.* as *L. meridionalis* (CHR); ibid., off track along E branch of Eglinton River, SE of Mt. Eglinton, NNE of Te Anau, 440 m, *Engel 18753*–c. ♂ + per. (F); ibid., Expectation Stream, *Zotov s.n.* (CHR); ibid., Lake Gunn, Eglinton Valley, ca. 365 m, *Child H 2588A*–c. per. + ♂ (F). **OTAGO:** Near Taieri Mouth, *Allison H 5198*–c. ♂ (CHR); near and S of Dunedin, ca. 45 m, *Allison H 1379* (CHR); Dunedin, Town Belt, ca. 150 m, *Child H 1110* (F); Ross Creek, Dunedin, ca. 150 m, *Child H 5553* (F); Mt. Cargill, ca. 455 m, *Child H 768* as *L. bidentata*–c. ♂ + per., *H 784* (F); near Naseby, ca. 610 m, *Allison H 5939* (CHR); Fiordland Natl. Park, Martin's Bay, N of Lake McKerrow, *Hatcher 818*–c. per. + ♂ (F); Mt. Aspiring Natl. Park, Blue River, near confluence with Makarora River, NNE of Makarora, 310 m, *Engel 18909*–c. ♂ (F). **WESTLAND:** Pleasant Flat, Haast Pass Road, *Allison H 6844* (CHR); near township of Fox Glacier, 0.5–0.6 mi. from front of Fox Glacier, *Schuster 60178*–c. ♂ + sporo. (F); Turiwhate Falls on Route 73, *Engel 6524*–c. per. (F). **CANTERBURY:** Arthur's Pass Natl. Park, valley immediately below Punchbowl Falls, 760 m, *Engel 6877* (F). **NORTH ISLAND. WELLINGTON:** Wellington, Hawkins Hill, *Moss s.n.* (AK); Port Nicholson, *Lyall s.n.* (BM); near Martinborough, Wairarapa, *Mues NZ 49* (F); Tawa Flat, *Butler H 68* (CHR); Akatarawa, Waterfall Creek, *Braggins 84l455* (AK); Akatarawa Forest Park, *Mues NZ 84* (F). **HAWKE'S BAY:** Near Wairoa, *Sainsbury s.n.* (CHR); Wairoa, "Kiwi," *Hodgson 2851* (CHR). **GISBORNE:** Lake Waikare-iti, Waikaremoana, ca. 915 m, *Hodgson 631* (CHR), *s.n.* as *L. meridionalis* (F). **SOUTH AUCKLAND:** E of Waiotapu Valley, S of Rotorua, *Allison H 3498* (CHR); Urutawa State Forest, Waioeka Scenic Gorge, 38 km S of Opotiki, *Kantak et al. 135* (F); Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel 22122*–c. ♂ (F); Coromandel State Forest Park, Kauraeranga River, just SE of suspended footbridge, 150 m, *Engel 22298*–c. sporo. + ♂ (F). **NORTH AUCKLAND:** Auckland, *Kirk 133* (CHR); Waipoua Forest, Waipoua River, *Allison H 1615* (CHR). **TASMANIA.** Iron Creek, near Tier Gully, about 7 mi. S of Nugent on road to Sorell, ca. 150 m, *Norris 30456*–c. ♂ (F); St. Mary's Pass, The Glens Falls, ca. 275 m, *Weymouth 1255* as *L. longistipula* (F, G, HO), *1254* as *L. multipenna*, *1257* as *L. subemarginata* (HO); Blue Tier, ca. 730–825 m, *Weymouth 1365* as *L. macrostipula* (F, HO), *1366* as *L. macroloba* (HO, M); Adamsons Peak, *Rodway s.n.* (HO); Huon River, near Tahune Picnic Area, ca. 50–100 m, *Norris 26757* (F); Tahune Forest Reserve, off Pine Track, along Huon River, N of Hartz Mtn. Natl. Park, 70 m, *Engel 19932*–c. ♂ (F); Mt. Wellington, Pipeline Track, *Ratkowsky s.n.*–c. sporo. (F); ibid., ibid., below "Ferntree," *Ratkowsky 80l63* (HO); ibid., water intake pipeline, *Ratkowsky 79l97* (HO); ibid., St. Crispin's, ca. 610 m, *Weymouth 517* as *L. bridelii* (FI–c. ♂, HO), *517* as *L. macrostipula*, *528* as *L. heterophylloides*, *1171* as *L. macrostipula*–c. sporo. (HO), *s.n.* as *L. rotundistipula* (M); ibid., Deep Creek, ca. 490 m, *Weymouth 1510* as *L. macrostipula* (F, HO), *304* as *L. bridelii*–c. sporo. (FI), *288* as *L. subemarginata*, *509* as *L. oldfieldiana* (HO), *982* as *L. gunniana* (M), *s.n.* as *L. bridelii* (PC); ibid., Lenah Valley Track, 700 m, *Ratkowsky 77l155* as *L. lenta* (HO); ibid., S Trig., ca. 1220 m, *Ratkowsky 77l157* (HO); ibid., Fools Tarn, *Ratkowsky s.n.* as *L. lenta* (F); Myrtle Forest, SW of Collinsvale, ca. 2.3 km N of Collins Bonnet, 700 m, *Engel 12778*–c. per. + ♂ (F); Mt. Field Natl. Park, Russell Falls, *Rodway s.n.* as *L. macrostipula* (HO); Gordon River, Sir Johns Falls, just up river from Butler Is., sea level, *Engel 14692*–c. ♂ (F); Cradle Mtn.–Lake St. Clair Natl. Park, Mt. Rufus, 1000 m, *Ratkowsky 78l77* (HO); King River, ca. 30 m, *Weymouth 1441* as *L. oldfieldiana* (HO); Strahan, Hogarth Falls Rivulet, *Weymouth 1468* as *L. spongiosa* (HO); vicinity of Montezuma Falls, just off NE Dundas Tramway (abandoned), W of Williamsford, SW of Rosebery, 400 m, *Engel 16449*–c. ♂ + per. (F); Murchison River at Murchison Highway, *Norris 33723* (F); Great Western Tiers, Walls of Jerusalem Natl. Park, plateau area between Lake Loane and Wild Dog Creek, 1120 m, *Engel 20152* (F); ibid., ibid., Lake Loane, 1070 m, *Engel 20161* (F); Hellyer Gorge Picnic Area, *Norris 33885* (F); Claude Creek, at road from Gowrie Park to Parangana Dam, ca. 600 m, *Norris 32676* (F); Upper Meander River, *Rodway s.n.* as *L. macrostipula* (HO). **AUSTRALIA. VICTORIA:** Mt. Baw Baw Village, 24 km ENE of Noojee, 1400 m, *Streimann 36202* (NY). **A.C.T.:** Bimberi Range, Murrays Gap, 50 km SW of Canberra, 1550 m, *Streimann 9752* (CBG); Brindabella Range, head of Mosquito Creek, 46 km SW of Canberra, 1680 m, *Streimann 4214* (CBG). **NEW SOUTH WALES:** Diggers Creek, 24 kmNE of Mt. Kosciusko, 1500 m, *Streimann 5432*–c. per. (CBG); Eucumbene River, 26 km NW of Adaminaby, 1330 m, *Streimann 7512* (CBG); Bradley's Creek, flowing out of Yaouk Bill Range, southern tablelands, 1240 m, *Verdon 1741* (CBG); Cambarwarra, *Thorpe* as *L. geheebii* (G). **QUEENSLAND:** Without specific loc., *Dietrich* as *L. heterophylloides* (M).

Chiloscyphus novaezeelandiae **var.** ***meridionalis*** (Steph.) J. J. Engel

Lophocolea meridionalis Steph., Bull. Herb. Boissier 6(10): 888. 1906 (= Spec. Hep. 3: 113). *Chiloscyphus novaezeelandiae* var. *meridionalis* (Steph.) J. J. Engel, Contr. Univ. Michigan Herb. 18: 109. 1992. Type: New Zealand, "Insula meridionalis," Waimate (Canterbury), May 1901, *Beckett 2737* (G!–c. ♂).

Chiloscyphus dargonius Gottsche, Linnaea 28: 554. 1856, *syn. nov.* *Lophocolea dargonia* (Gottsche) Steph., Hedwigia 32: 327. 1893. Type: Australian Alps, near Dargo, *F. v. Mueller* (BM!–c. per., G!).

Plants appearing like phases of *C. austrigenus* or *C. semiteres* in dorsal view; leaf insertion mostly strongly recurved, weakly J-shaped; leaves often ± orbicular to oblate, as wide as high or wider than high; leaf apices slightly variable: broadly rounded to truncate, sporadically retuse but never developing lobes, the apices (and at times the margins) often minutely and regularly crenulate by convex exposed walls; leaf cell trigones often small and concave sided to medium and straight sided; median leaf cells 22–35 µm wide × 31–40 µm long; oil-bodies 2–3 per cell, slightly papillose to coarsely botryoidal and with segments well-defined. Underleaf margins to 3(4)-dentate-laciniate. Gemmae sporadically present.

Variation—Weak phases may have some shoots with more deeply divided underleaves. These phases should be treated with care to avoid confusion with *C. semiteres*. Careful search should be made for underleaves that have the diagnostic characters of the species (i.e., concavity and shallow sinus).

Notes on Type Specimens—1) *Lophocolea meridionalis* Steph. Plants are well-developed and androecial shoots are common. Leaf apices for the most part are undulate, undivided, broadly rounded to truncate and entire and lend the shoots an appearance in dorsal aspect like that of *C. austrigenus* subsp. *okaritanus*. Apices are only sporadically "brevissime inciso-biloba" as stated in the protologue (Stephani, 1898–1924 [1906], p. 113). However, underleaves are typical of *C. novaezeelandiae*, being bifid to ca. 0.3–0.5, with the lamina margins on each side often having a dentiform-laciniiform process. The shoots appear similar to Fig. 29: 9 in ventral view.

2) *Chiloscyphus dargonius* Gottsche. I have seen 2 collections—one at G consisting of 3 sterile shoots, the other at BM consisting of ca. 8–10 shoots, 3 bearing gynoecia, but only 1 having a ± mature perianth. The specimens are flaccid and represent a suboptimal phase of *C. novaezeelandiae* var. *meridionalis*. The plants probably grew in a particularly damp and/or shady niche for the species, a factor accounting for atypical character expression. Under such conditions *C. novaezeelandiae* in general has underleaves that are more deeply bifid (to. 0.4–0.8), plane or feebly concave, and free or sporadically connate on 1 side. Trigones are minute to medium (I could find no trace of bulging trigones). Gynoecia occur on leading shoots. The innermost bracteole is slightly smaller than the bracts, ± orbicular, deeply concave, the margins are strongly reflexed and on each side bear a small tooth, and the apex is bifid to ca. 0.2. The single perianth is narrowly and sharply trigonous from the base to ca. 0.6 the perianth length, which is the point where the lobes become free. Distal to that point each lobe member flares, lending the perianth a campanulate shape (the protologue states the perianths are "prismatico triangulari-campanulato"). Perianth lobes are shallowly bifid, the segments are irregular and vary from rounded to broadly acute to apiculate. The lobes otherwise have a few, irregular, dentiform to laciniiform processes below the level of the segments. The atypical perianth shape is likely due to the suboptimal niche in which the plants occurred.

Distribution and Ecology—The variety occurs in New Zealand (South Is., 15–870 m; North Is., 670 m), Australia: Tasmania (sea level–1050 m), New South Wales (1280–1500 m).

The var. *meridionalis* is nearly exclusively associated with watercourses in forests, and on the whole occupies niches wetter than those for var. *novaezeelandiae*. Plants of var. *meridionalis* often grow on rock or wood that is submerged or that occurs within the flood zone. It occasionally is subalpine in Tasmania, and occupies niches similar to var. *novaezeelandiae*.

The variety rarely occupies mesic niches, but may be found on clayey soil in forests, for example under *Leptospermum ericoides* (kanuka).

Specimens Seen (selected)—**NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, Borland Road, 14 km by road WNW from Borland Lodge, near S branch of Borland Burn, W of Monowai, 855–870 m, *Engel 18705*–c. ♂ (F); ibid., head of Lake Manapouri to Wilmot Pass, *Simpson s.n.*–c. per. (CHR); ibid., Lake Marian Track, on Hollyford River, at foot of Mt. Christina, *Schuster 55707* (F). **OTAGO:** Dunedin, Mornington, *Allison H 1392* (CHR); ibid., Cosy Dell, ca. 215 m, *Child H 1646* (F); Rock and Pillar, ca. 760 m, *Child H 3022* (F); Fiordland Natl. Park, trail between Gunn's Hut and Hidden Falls, ca. 30 mi. SE of Lake McKerrow, *Hatcher 616* (F); ibid., head of Lake McKerrow, *Hatcher 909* (F). **WESTLAND:** Franz Josef Glacier, N side of Waiho River Valley, ca. 150–215 m, *Schuster 67-4200*–c. per. + ♂ (F); Camp Creek, W of Alexander Range, 400 m, *Reif C76* (F); Westland Natl. Park, S margin of Lake Wahapo, *Engel 6708* (F); Turiwhate Falls on Route 73, *Engel 6523*–c. per. + ♂ (F). **CANTERBURY:** Waimate, *Beckett s.n.* as *L. heterophylloides* (M). **NELSON:** Paparoa Range, N side of gorge of Fox River, NE of Punakaiki, 15 m, *Engel 19107* (F). **MARLBOROUGH:** Pelorus Bridge Scenic Reserve, Rai River, ca. 30 m, *Fife 5741* (F); Pelorus Bridge, *Braggins s.n.* (AK); ibid., Circle Track, *Braggins s.n.* (AK); below Pelorus Bridge, *Braggins s.n.* (AK). **NORTH ISLAND. WELLINGTON:** Western Ruahine State Forest, Oroua Valley, ca. 670 m, *H. Hodgson s.n.* (CHR). **TASMANIA.** N of St. Marys Pass, on coastal highway, *Norris 32325A* (F); W bank of Pearly Brook, 60 m, *Rowlatt 94A* (F); Tahune Picnic Area Nature Trail, ca. 50–100 m, *Norris 29983* (F); Mt. Wellington, ca. 425 m, *Rodway s.n.* as *L. bridelii* (HO); ibid., Ridgeway Reservoir, *Ratkowsky 80172* (HO); ibid., Pipeline Track, *Ratkowsky s.n.* (F); ibid., Lower Pipeline, *Ratkowsky s.n.* as *L. subporosa*–c. per. + ♂ (F); ibid., St. Crispins, ca. 625 m, *Weymouth 1171b* as *L. brevis*–c. sporo. + ♂ (F, HO); ibid., Deep Creek, ca. 490 m, *Weymouth 303* as *L. bispinosa*–c. sporo. + ♂, *1524* as *L. macrostipula* (HO); ibid., Myrtle Forest Creek, *Ratkowsky 80169* (HO); Myrtle Forest, SW of Collinsvale, N of Collins Bonnet, 750 m, *Engel 13206* (F); near Jacques Creek, near end of Styx River Road, *Norris 29038* (F); Mt. Field Natl. Park, along Tyenna River near campground at National Park, ca. 200 m, *Norris 28816* (F); ibid., Russell Falls, *Rodway s.n.* as *L. oldfieldiana* (HO); Gordon River, Sir John Falls, just up river from Butler Is., sea level, *Engel 14695A*–c. ♂, *14698* (F); ibid., Expectation Reach, between Horseshoe Bend and abandoned HEC hut, sea level–50 m, *Engel 14822* (F); Cradle Mtn.–Lake St. Clair Natl. Park, Mt. Rufus, *Ratkowsky 7919* (HO); along Franklin River, at Frenchman's Cap Trail crossing, ca. 400 m, *Norris 31209* (F); King River, *Rodway s.n.* as *L. bridelii* (HO); ibid., *Moore s.n.* as *L. multipenna* (M); Purgatory Gap, S of Queenstown, *Norris 33605* (F); vicinity of Montezuma Falls, just off NE Dundas Tramway (abandoned), W of Williamsford, SW of Rosebery, 400 m, *Engel 16444*–c. ♂ (F); Great Western Tiers, plateau near Lake Salome, W of Walls of Jerusalem, 1050 m, *Engel 15958* (F); Leven Gorge, along River Leven, 10 km by road from Nietta, SSE of Burnie, 400 m, *Engel 15759* (F); Emu (Companion) River, near Guildford Road, SSW of Burnie, 500 m, *Engel 15841*–c. ♂ (F); track from Ferndene to Mt. Dial, SSW of Penguin, SE of Burnie, 30–60 m, *Engel 15602*–c. ♂ (F); Ferndene, *Norris 33984* (F). **AUSTRALIA. NEW SOUTH WALES:** Diggers Creek, 24 km SE of Mt. Kosciusko, 1500 m, *Streimann 5431* (CBG); 1 km SW of Cabramurra, 1500 m, *Streimann 7386* (CBG); Gloucester River, 35 km WSW of Gloucester, 1280 m, *Streimann 6367* as *L. semiteres* (CBG).

Chiloscyphus novaezeelandiae **var.** ***grandistipulus*** (Schiffn.) J. J. Engel

Lophocolea grandistipula Schiffn. *in* Naumann, Forschungsr. Gazelle 4: 12. *pl. 3, f. 29–32*. 1890. *Chiloscyphus novaezeelandiae* var. *grandistipulus* (Schiffn.) J. J. Engel, Contr. Univ. Michigan Herb. 18: 110. 1992. Type: New Zealand, Auckland, 8. 11. 1875, *Naumann* (FH!, sub *L. stipularis*, *nom. hb.*).

Lophocolea rotundistipula Steph., Bull. Herb. Boissier 6(9): 793. 1906 (= Spec. Hep. 3: 93), *syn. cf.* Hodgson (1953), *non L. rotundistipula* Steph., K. Svenska Vetenskapsakad Handl. 46 (9): 52. 1911 (= *Clasmatocolea puccioana* (De Not.) Grolle; cf. Engel, 1980). Type: New Zealand, Auckland, *Helms s.n.* (G!–c. per.).

Lophocolea australis Gottsche, Linnaea 28: 553. 1856, *syn. nov.* ≡ *Lophocolea austro-alpina* Steph., Bull. Herb. Boissier 6(10): 876. 1906 (= Spec. Hep. 3: 101), *nom. illeg. Chiloscyphus austro-alpinus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 411. 1985 (1984), *nom. illeg. non L. australis* (Gottsche, Lindenb. & Nees) Mitt. *in* Hooker f., Bot. Antarc. Voy. 3: 226. 1859 (≡ *Chiloscyphus australis* Gottsche, Lindenb. & Nees, Syn. Hep. 189. 1845 (≡ *Leptoscyphus australis* (Gottsche, Lindenb. & Nees) R.M. Schust.). Lectotype (*nov.*): Australian Alps, without specific loc., *F. von Mueller* (MEL!–c. sporo. + ♂); isolectotypes: (BM!, MEL!–c. sporo.; S![2]–c. per.).

Lophocolea kirkii Steph., Bull. Herb. Boissier 6(10): 879. 1906 (= Spec. Hep. 3: 104), *syn. cf.* Hodgson (1953). Type: New Zealand, Great Barrier Is., *Kirk 161* (G!–c. per. + ♂).

Branching often predominantly to exclusively intercalary, exceptionally with terminal and intercalary branch types of equal frequency. Leaf insertion not or weakly recurved; leaves often ovate and longer than wide, the apices nearly exclusively bilobed; leaf cell trigones often small to medium, concave to straight sided, less frequently large and bulging; median leaf cells 14–22 µm wide × 16–26 µm long; oil-bodies 2, very exceptionally 3 per cell, coarsely botryoidal and with segments well-defined. Underleaf margins to 2-dentate-laciniate. Gemmae sporadically present.

Notes on Type Specimens—1) *Lophocolea grandistipula* Schiffn. The specimen, which bears the name *Lophocolea stipularis* Schiffn. (nom. hb.), consists of small, flaccid, sterile plants. Leaves are consistently bifid, have gemmae at the lobe tips and have erose lobes in median and basal shoot sectors. The ventral and sometimes the dorsal leaf margins have a few small teeth (see sub. Variation, p. 77). Underleaves are concave and bifid to ca. 0.4–0.5. Trigones are medium and straight sided to weakly knot-like.

2) *Lophocolea rotundistipula* Steph. (Stephani, 1898–1924 [1906]). The type consists of 2 shoots, each bearing a well-developed perianth (each shoot being stored in a separate micropacket). One shoot served as the basis for the Stephani icon (*Lophocolea* no. 138). Apices of leaves and bracts are consistently bilobed, as shown in the Stephani icon. Bracteoles are ovate to orbicular and distinctly bifid, and not wide obovate and with the apex irregularly spinulose, as stated in the protologue. Leaf cell trigones are medium and straight sided and not "subnullis" as stated by Stephani (1898–1924 [1906], p. 93).

3) *Lophocolea austro-alpina* Steph. (≡ *Lophocolea australis* Gottsche). The plants are in rather poor condition probably because of improper drying. Leaves are strongly dorsally assurgent, often ± subvertical, and broad based. Most shoots have leaves consistently shallowly bilobed, but a few shoots have leaf apices varying from broadly rounded to truncate to 1-lobed to shallowly bilobed. Trigones are distinct and medium and straight sided. Underleaves are concave, bifid to 0.4–0.7(0.8), and the disc has a dentiform to laciniiform process on each side. The trigonous perianths usually have some or all parts of the mouth missing. A few perianths have sufficient portions remaining intact to ascertain that the lobes are distinctly bifid and have a few accessory teeth. Bracts and bracteoles are short-bilobed; the bracteoles are subequal to bracts in size, concave, and orbicular. All observed specimens are admixed with a moss and *Riccardia* sp.

4) *Lophocolea kirkii* Steph. The specimen consists of somewhat flaccid yet well-developed plants with consistently bifid leaves and distinctly concave underleaves, the latter ca. 0.3–0.5-fid. A few leaves have toothed margins and erose apices typical of gemmiparous shoots. Trigones are small and concave sided to medium and straight sided, and not absent as stated in the protologue.

Distribution and Ecology—The var. *grandistipulus* occasionally occurs in New Zealand (Stewart Is.; South Is., 260–850 m; North Is., 45–185 m), and in Australia is rare in Tasmania (200 m) and is also rare in New South Wales (1600 m).

The var. *grandistipulus* occurs in watercourses, but seems less common than the other two varieties. In watercourses of forests, plants occupy niches similar to those of var. *novaezeelandiae*. The variety is unique for the species in occurring in alpine sites (though rarely and then only in New South Wales) and may be found on shaded moist creek banks in otherwise open, hummock alpine grasslands. On Stewart Is. immediately below Belltopper Falls at Port Pegasus plants form small colonies on bedrock in an open, humid niche dominated by bedrock with a forest margin of *Weinmannia racemosa* and *Dracophyllum*. The variety is rather morphologically uniform at this site.

The variety occasionally occupies mesic niches such as damp shady rocks in gorges, damp roadside places and even on logs in forests.

Specimens Seen (selected)—**NEW ZEALAND. STEWART ISLAND:** Port Pegasus, immediately below Belltopper Falls, North Arm, ca. 5 m, *Engel, von Konrat & Braggins 24120* (F). **SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, Expectation Stream, *Zotov s.n.* (CHR); ibid., chasm of Cleddeau River, above Milford Sound, *Schuster 49367* (F). **OTAGO:** Fiordland Natl. Park, Lake Howden, ca. 610 m, *Child H 2564* (F). **CANTERBURY:** Banks Peninsula, valley NE of Te Oka, on Kinloch Road, 260 m, *Fife 6815* (F); ibid., Kaituna Valley, *Hatcher 1213E*–c. sporo., *1851*–c. sporo. (F); Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel 18451*, *18452*–c. per., *18479*–c. ♂ (F). **NELSON:** Nelson Lakes Natl. Park, NE margin of Lake Rotoroa, 520 m, *Engel 21524*–c. per. + ♂ (F). **NORTH ISLAND. WELLINGTON:** Wellington, Miramar (Watts Peninsula), ca. 45 m, *Braggins H 31*–c. sporo. + ♂ (AK); Wiltons Bush, *Mason s.n.* as *L. kirkii* (CHR); Orua River, near Apito, NE of Kimboltons Fielding, *Zotov 7019* (CHR). **HAWKE'S BAY:** McKinnon's Bush, near Wairoa, *Hodgson 185*–c. ♂ (CHR); Wairoa, "Kiwi," *Hodgson 209* (CHR). **GISBORNE:** Lake Waikaremoana, *Hodgson 126* (CHR); ibid., *Butler 2042* (CHR); ibid., Wairaumoana, *Sainsbury s.n.*–c. ♂ + per. (CHR). **TARANAKI:** Mt. Messenger, ca. 185 m, *Allison H 3483* (CHR). **SOUTH AUCKLAND:** Mangaiti Gorge, near Atiamuri, *Allison H 3367* (CHR). **LITTLE BARRIER IS.:** Parihakoakoa Stream, *Braggins et al. 80/44* (AK). **TASMANIA.** Above Burns Creek, immediately N of boundary with Richmond Municipality, ca. 200 m, *Norris 30745* (F). **AUSTRALIA. VICTORIA:** Mt. Baw Baw, *Scott s.n.*–c. sporo. + ♂. **NEW SOUTH WALES:** Emu Plains, Cabramurra–Khancoban Road, 39 km NE of Khancoban, 1600 m, *Streimann 7391* as *L. bispinosa* (CBG).

Chiloscyphus hattorii J. J. Engel

Chiloscyphus hattorii J. J. Engel, J. Hattori Bot. Lab. 74: 29. *f. 1–2.* 1993. Holotype: New Zealand, South Is., Fiordland Natl. Park, Doubtful Sound, Elizabeth Is., 50–150 ft, *Schuster 52852* (F); isotype: (CHR).

Plants rather flexuous, prostrate, pale green, nitid when dry; shoots to 2 mm wide. Branches exclusively lateral intercalary, from ventral end of leaf axil (often originating in "axil" of leaf–underleaf connation); terminal branching very rare (1 branch seen). Stems rather narrow for plant size, 8–9 cells high, the cortex poorly differentiated, in a single layer of slightly thicker walled cells; medullary cells thick walled. Rhizoids from stem at immediate base of underleaves, often in dense, cylindric fascicles, the rhizoid tips often branched. Leaves with the general form of *C. semiteres*, alternate, dorsally assurgent, widely spreading, imbricate, free dorsally, orientation strongly succubous, the insertion slightly and abruptly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves overall convex but often with an adaxial concavity in basal sector, subsymmetrically wide ovate, the apex often broadly and gently deflexed, polymorphic: rounded to truncate to retuse to 1-lobed to shallowly bilobed, the apex otherwise entire; dorsal margin broadly curved, especially in basal half, often at least locally deflexed, entire, somewhat decurrent; ventral margin broadly curved, commonly more strongly so than dorsal margin, plane, entire but occasionally with a sharp tooth in basal third. Leaf cells with walls thin, trigones medium and straight sided to large and bulging, median cells 23–31 µm wide, 28–32 µm

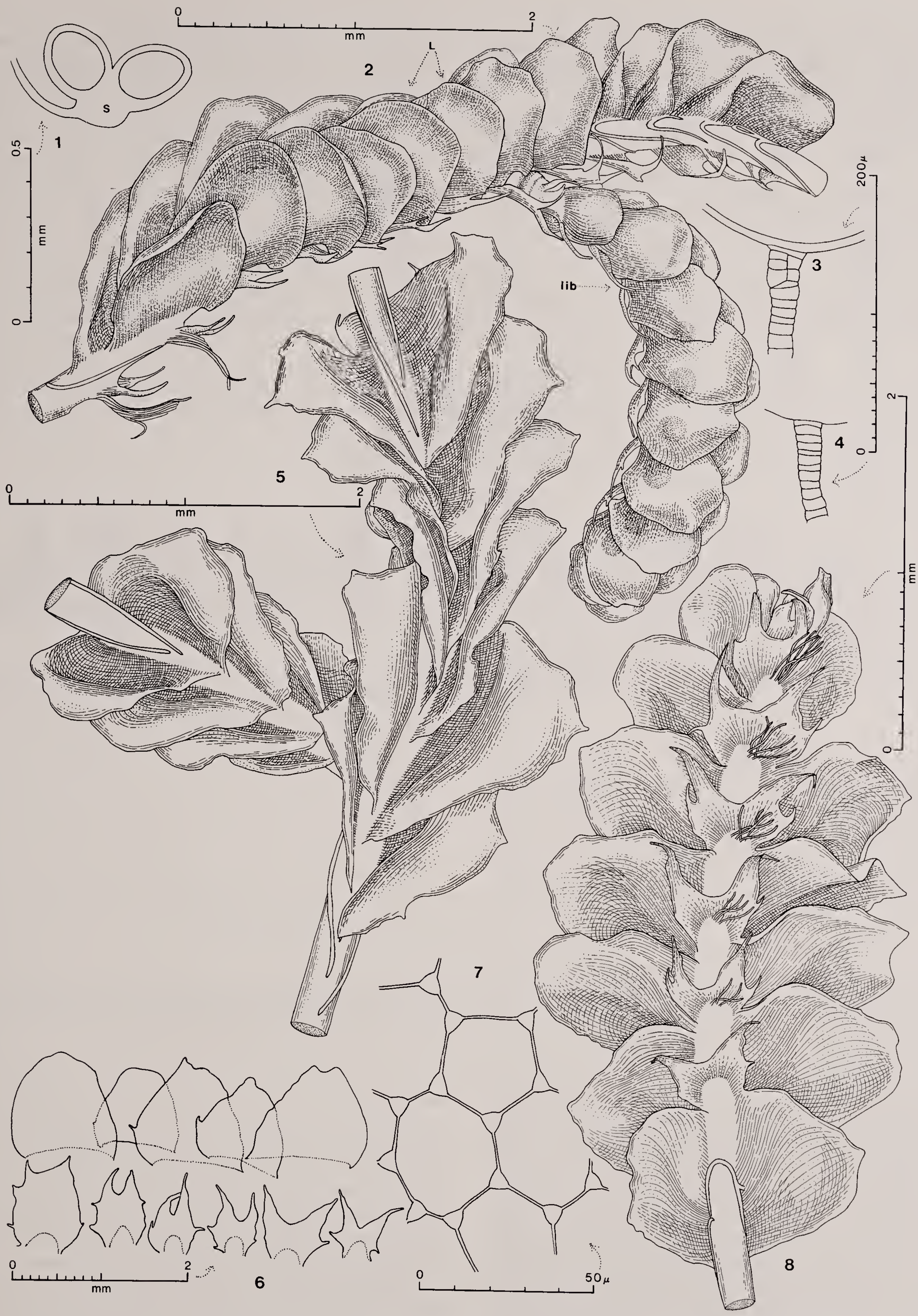

FIG. 31. *Chiloscyphus hattorii* J. J. Engel. **1.** Opposing antheridial bracts with stem (= s), cross section. **2.** Leading shoot with a subfoliose androecium and a lateral-intercalary branch (= LIB) that also bears a subfoliose androecium, lateral view. The first leaves on main shoot to form ♂ lobule flaps are indicated by the symbol "L," the distal 4 bracts on the side facing viewer have been removed to reveal adaxial face of exposed bracts and insertion of bracts on side nearest viewer (note fusion of lobule bases). Note that branch issues from lateral portion of underleaf axil. **3, 4.** Two antheridial stalks, at bottom unistratose throughout, at top locally bistratose. **5.** Sector of shoot with lateral-intercalary branch (at left); note variation of leaf apices. **6.** Leaf and underleaf outlines, all from one sterile shoot. **7.** Median leaf cells. **8.** Sector of main shoot, ventral view. (**1, 3–8,** from *Schuster 52852*, New Zealand, South Is., Elizabeth Is.; **2,** from *Schuster 55467*, New Zealand, South Is., 0.6–0.7 mi. S of Haast Pass.)

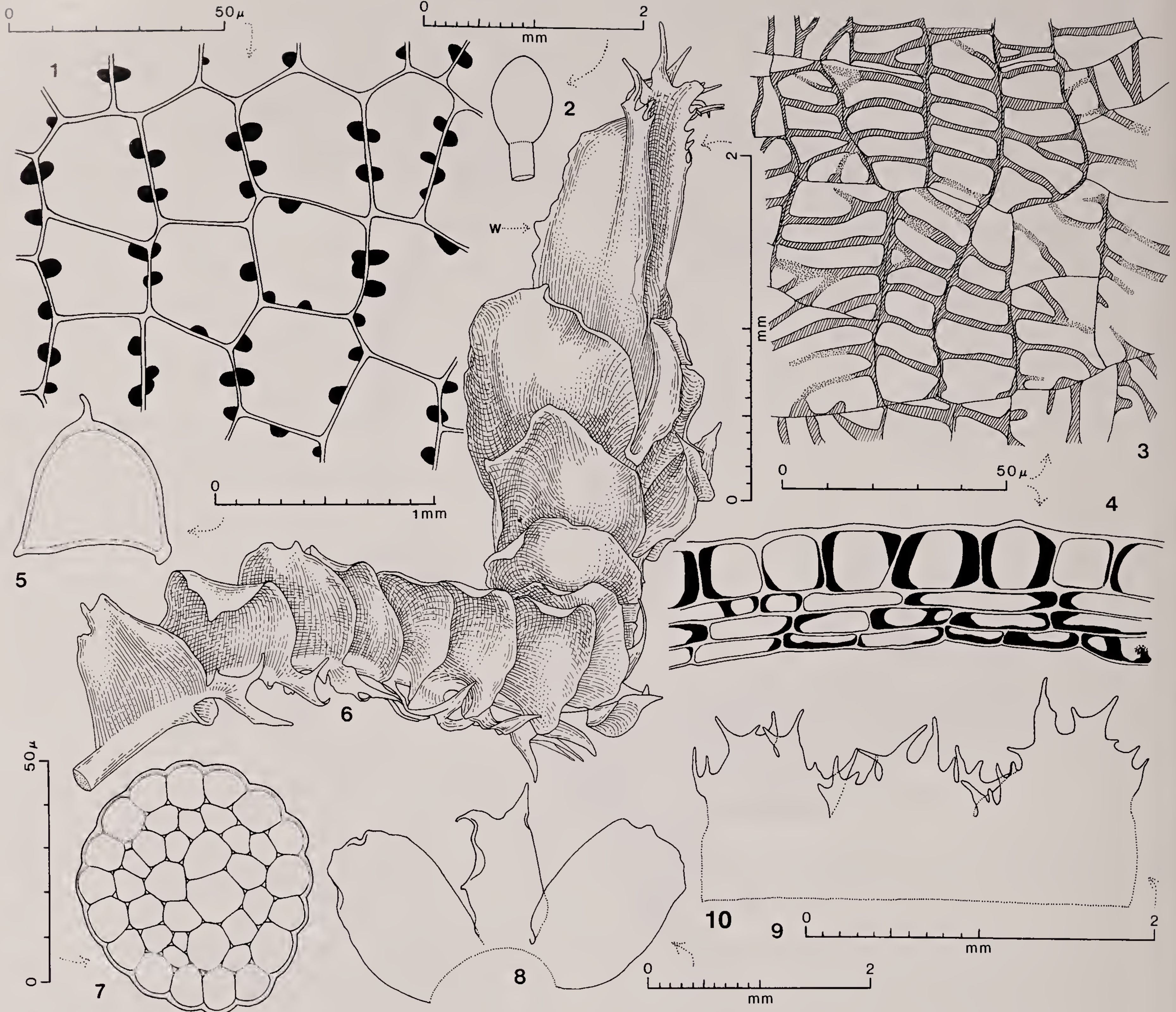

FIG. 32. *Chiloscyphus hattorii* J. J. Engel. **1.** Capsule wall, outer layer. **2.** Capsule profile. **3.** Capsule wall, inner layer. **4.** Capsule wall, cross section. **5.** Perianth, cross section. **6.** Perianth bearing shoot; note connation of innermost bract and bracteole and variation of leaf apices (w = wing), lateral-ventral view. **7.** Seta, cross section. **8.** ♀ Bracts, and in middle, bracteole. **9.** Perianth mouth, ventral lobe in middle. (All from *Schuster 52852*, New Zealand, South Is., Elizabeth Is.)

long; surface smooth. Oil-bodies ± colorless, 3–6 per cell, 3.8–4.5 × 5–6.5 to 5–5.5 × 10 μm, coarsely papillose, rough externally. Underleaves much smaller than leaves, 1.6–2.8× stem width, narrowly connate on 1 or both sides, the insertion often asymmetric, inverted U-shaped, the underleaves moderately spreading, contiguous to loosely imbricate, convex (ventral view) and with the lobes broadly arching dorsally, the underleaves narrowly ovate to subrectangular when lobes ± parallel, ± obtrapezoidal when lobes widely diverging, bifid to (0.2)0.4–0.7(0.75) by a variably shaped sinus; lobes acuminate to subcaudate, sporadically narrowly acute-subcuspidate, the lobe margins entire; lamina margins 1–2-dentate to subciliate to occasionally laciniate.

Asexual reproduction absent.

Plants dioecious. Androecia on main shoot or leading branches, indeterminate, subspicate to subfolious (even on same shoot); bracts somewhat to distinctly smaller than leaves, hardly more erect or dorsally assurgent than leaves, loosely to rather tightly appressed to bract immediately above, the saccate portion crenulate in profile and fused toward base with opposite bract, the bracts ventricose in basal portion, the distal portion reflexed and convex, the apex usually broadly rounded to truncate, less variable than in leaves, the ventral margin entire; lobule margin inflexed to involute, rounded and with a few small and at times prominent teeth and slime papillae, or edentate and merely with a simple or stalked slime papilla; antheridia solitary, the stalk 10–12 cells long, uniseriate throughout or mostly uniseriate but with a few biseriate areas. Gynoecia on main shoot or leading lateral-intercalary branches; subfloral innovations occasional, from axil of bract of lowermost series. Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free from one another or feebly connate with each other, with an adaxial concavity toward the base but slightly convex distally, ovate to subrectangular; apices often undulate, grading from truncate to repand-dentate to shallowly bilobed, otherwise entire, at most with an accessory tooth; lamina margins ± evenly arched, undulate, locally sharply reflexed, entire. Bracteoles of innermost series of ± similar length to bracts but somewhat narrower, broadly connate on 1 side, lesser so on the other, distinctly concave and with margins broadly reflexed, narrowly ovate to subrectangular; apices bifid to ca. 0.3, the lobes canaliculate, acuminate, entire; lamina margins entire or with a few small teeth. Perianth moderately to longly exserted beyond bracts, sharply trigonous throughout but the sides often infolded or slightly bulging, the perianths narrowly oblong to elliptic, not or slightly narrowing toward the wide, rather deeply 3-lobed mouth; lobes rather deeply bifid, the segments acuminate, entire or 1–2-dentate-laciniate; keels sharply angular to slightly rounded, with keelar wings rather common, of a few to several cells high, unarmed or with a few small teeth. Calyptra small, ca. 0.75× perianth length at maturity.

Seta 6 cells in diam., with 17 rows of outer cells surrounding a subepidermal layer of somewhat smaller cells, the innermost core made up of 4–5 cells subequal to or slightly larger than epidermal cells, the inner cells with corners as in large, bulging trigones. Capsule elliptic, 735 µm × 560 µm, the wall 26–31 µm thick, of 4 layers, the outer layer of cells equal to thickness of all of interior strata; outer layer of cells subquadrate to short rectangular, the radial walls with red-brown thickenings that are nodular but never spine-like, the thickenings mostly on longitudinal walls and sometimes on transverse walls; innermost layer of cells irregularly quadrate to subrectangular, the vertical radial walls with somewhat thick continuous sheets of red-brown wall material, with semiannular bands red brown, common, narrow, sometimes incomplete, sometimes forked, the radial walls with nodular thickenings sporadic or lacking.

Spores 10.1–11.5 µm, pale yellow brown, thin, with faint, low but sharply defined, rather close papillose and short-vermiculate markings, spore:elater diameter ratio 1.1–1.4:1. Elaters tortuous, 8.2–9.6 µm wide, the spirals 1.9–2.4 µm wide.

DIFFERENTIATION—This species differs from *C. novaezeelandiae*, its closest relative, by the convex underleaves (ventral view; Fig. 31: 9); the absence of terminal branching, all branches being lateral-intercalary (Fig. 31: 2, 5); the greater oil-body number per cell, being 3–6; the smaller spores; the lack of gemmae, and the often undivided and entire bract apices (Fig. 32: 6, 8).

VARIATION—*Hatcher 1582* and *1638* from Stewart Is. consist of shoots with young gynoecia that innovate. Each of the innovations in turn produces a gynoecium that innovates, the shoots thus repeatedly innovating. Leaf apices in these populations are broadly rounded to truncate, with minimal variability. The combination of underleaf characters and complete absence of terminal branching will place the plants in *C. hattorii.* Sterile shoots were not observed.

NOTE—Long periods of time were spent in the study of branching in this complex. Only one *Frullania*-type branch could be found for *C. hattorii*; it occurred in *Hatcher 1583*. Branching in this species, with the solitary exception just mentioned, is solely lateral-intercalary. The branch position is variable, but not to the extent found in *C. novaezeelandiae* (see p. 79). In *C. hattorii* lateral-intercalary branches arise from near the ventral end of the leaf, sometimes in the axil of the ventral sector of the leaf but more often in the "axil" of the leaf–underleaf connation. This grades to the edge of the underleaf axil, and to ventral/ventral-lateral and then in the axil of half of the underleaf (Fig. 31: 2). True ventral-intercalary branches—from the median portion of the underleaf axil—could not be found.

DISTRIBUTION AND ECOLOGY—Known from Stewart Is., Southland and Otago Provinces on South Is. (15–520 m), and one site (Coromandel Pen.) on North Is. (305 m). The species occurs on decayed, moist logs in forests. The type is from a *Nothofagus–Dacrydium cupressinum–Metrosideros robusta* forest. The ecology of this species seems to complement that of *C. novaezeelandiae*, which nearly always is associated with watercourses or waterfalls.

SPECIMENS SEEN—**NEW ZEALAND. STEWART IS.:** Half Moon Bay, near Oban, *Hatcher 1638* (F); between Half Moon Bay and Deep Bay, *Hatcher 1582*, *1583* (F). **SOUTH ISLAND. OTAGO:** 0.6–0.7 mi. S of Haast Pass, ca. 505–520 m, *Schuster 55467*–c. ♂ + per. + sporo. (F). **NORTH ISLAND. SOUTH AUCKLAND:** Coromandel Peninsula, ca. 2 mi. SW of Manai, ca. 305 m, *Schuster 67-3882* (F).

Chiloscyphus calcareus (Steph.) J. J. Engel & R. M. Schust.

Lophocolea calcarea Steph., Bull. Herb. Boissier 6(10): 884. 1906 (= Spec. Hep. 3: 109). *Chiloscyphus calcareus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 412. 1985 (1984). Type: New Zealand, without specific loc., ex herb. Kew, *Colenso 2023* (BM = *absens*, G!–c. per.).

Lophocolea wairoae Herzog, Trans. & Proc. Roy. Soc. New Zealand 65: 354. 1935, *syn. fide* Hodgson (1953). Holotype: New Zealand, North Is., Whakamahia, Wairoa, Easter, 1932, *Hodgson 123* (JE!); isotype: (CHR!).

Plants wire-like, brittle, fragile, prostrate to somewhat ascending, pale green to pale brown; shoots small, 0.5–1 mm wide. Branches common, mostly of *Frullania* type, occasionally lateral intercalary. Stems 9–10 cells high, the cortex moderately differentiated, in a single layer of somewhat thick-walled cells moderately larger than medullary cells; medullary cell walls slightly thickened. Rhizoids scarcely developed, from stem at base of underleaves. Leaves rather rigid, alternate, strongly dorsally assurgent and often subvertical/vertical, widely spreading, loosely imbricate (distant to contiguous on smaller shoots), free dorsally, orientation strongly succubous, the insertion not to feebly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells (the insertions of opposing leaves often extending to the dorsalmost laterally juxtaposed rows of stem cells and not to exact midpoint of stem). Leaves slightly convex to plane to slightly concave (never conchiform concave), ± symmetrically wide ovate to wide elliptic; apex fundamentally undivided, variable: broadly rounded to truncate to retuse to short bilobed, the lobes, when present, usually rounded, sporadically acute but not sharply so, the apex otherwise entire; margins broadly and ± evenly curved, entire, the dorsal plane to slightly deflexed, the ventral plane. Leaves bordered by 1 or sometimes locally 2 rows of somewhat larger (in length and often width) cells. Leaf cells with walls thin, trigones well developed, medium and straight sided to knot-like, median leaf cells 18–26 µm wide and long; surface smooth. Underleaves much smaller than leaves, 0.9–1.8× stem width, free or very narrowly connate on 1 side, the insertion crescent to shallowly inverted U-shaped, the underleaf disc somewhat spreading, the lobes arching dorsally toward stem, the underleaves distant to contiguous, plane to convex (ventral view), ovate to subrectangular; apex bifid to (0.5)0.65–0.85, the lobes ± parallel to somewhat diverging, acuminate, terminating in a uniseriate row of 2–4 cells, the lobe margins entire; lamina margins plane, entire or with a dentiform to ciliiform to sporadically small laciniiform process on each side.

Asexual reproduction absent.

Plants dioecious. Androecia on main shoots or, sporadically, rather short *Frullania*-type branches; androecia subfolious, not sharply differentiated from vegetative sectors; bracts somewhat smaller than leaves, suberect, vertical, dorsally assurgent, rather tightly appressed to bract immediately above, the saccate portion smooth in profile and fused toward base with opposite bract, the bracts ventricose in basal half, the distal portion distinctly concave, the apex broadly rounded to truncate to retuse, the ventral margin entire; lobule large for bract size, the margin inflexed, the distal sector rounded to acute, the free margin sparingly crenate and with a few slime papillae; antheridia solitary, the stalk uniseriate. Gynoecia on main shoot. Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free from one another, convex, narrowly ovate; apices variable: truncate to retuse and with 2 low, rounded, entire lobes, to distinctly bifid by acute, entire lobes; lamina margins ± evenly arched, plane to slightly deflexed, entire or, sporadically, with a tooth. Bracteoles of innermost series somewhat smaller than bracts, at times ± equal to bracts in length but narrower, free or narrowly connate on 1 side, slightly concave, ovate to less often subelliptic; apices bifid to ca. 0.35 by ventrally sulcate, acute to acuminate, entire-margined lobes; lamina margins reflexed, entire. Perianth longly exserted beyond bracts, rather sharply trigonous throughout, the sides sporadically feebly convex, the perianths obovate to oblong, sporadically ovate, not or slightly expanding toward the wide, deeply 3-lobed mouth; lobes free for ca. 0.3–0.4 the perianth length, distinctly bifid, the segments medium acute to acuminate, entire or occasionally with a tooth, the lobes otherwise coarsely dentate-laciniate below level of segments; keels sharp, with keelar wings common, often short, of a few cells high and entire or sparingly armed.

Seta 6–7 cells in diam., with 19 rows of outer cells surrounding an inner core of scattered cells subequal to or somewhat smaller and with corners thickened as in minute trigones. Capsule wide elliptic, 525–560 µm × 455–490 µm, the walls 42–43 µm thick, of 4 layers, the outer layer of cells equal to thickness of all of interior strata; outer layer of cells short rectangular, the radial walls with red-brown nodular to spine-like thickenings on some but not all longitudinal walls and only sporadically on transverse walls, the outer wall with weak tendency toward two-phase type of distribution of thickenings (i.e., longitudinal walls with rather dense thickenings alternating with those with few or no thickenings), the outer layer with semiannular bands present, sporadic; intermediate layers each slightly thicker than inner layer, with vertical thickenings often considerably tangentially extended; innermost layer of cells long rectangular, with semiannular bands red brown, common, narrow, sometimes incomplete, the radial walls with nodular thickenings often present on longitudinal walls.

Spores 13.5–15.4 µm, pale brown, thin, with dense, low but sharply defined, close papillae and short-vermiculate markings, the spore:elater diameter ratio 1.6–2.1:1. Elaters tortuous, 6.7–8.6 µm wide, the spirals 2.4–2.9 µm wide.

DIFFERENTIATION—This rarely cited species has an interesting history. Stephani described the species early last century (Stephani, 1898–1924 [1906]), but it was not subsequently cited until Hodgson (1953) recognized and treated the plant. However, Hodgson (1962, 1965, p. 79) placed the species in the synonymy of *Lophocolea minor* Nees, a holarctic, universally gemmiparous species. A number of collections from CHR determined as *L. minor* were studied and these serve to illustrate that the species was in part misunderstood. All specimens occurring on a limestone substrate are *C. calcareus*. Collections from noncalcareus substrates are misdeterminations of several different species of *Chiloscyphus* as well as other genera (*Lethocolea*, *Hepatostolonophora*, *Heteroscyphus*, *Leptoscyphus*).

The pale brown color and well-developed trigones of *C. calcareus* immediately suggest *Leptoscyphus*. However, gynoecial symmetry precludes placement in that genus. Perianths are trigonous (and lack reduction in length or width of the ventral lobe); bracteoles are well-developed and may be subequal to the bracts in length but somewhat narrower. Brown coloration may not occur in living plants, and this feature requires confirmation with fresh material.

Chiloscyphus calcareus is similar to *C. hattorii*, sharing with that species plane to convex underleaves and absence of gemmae. It differs from that species by the characters cited in the key.

VARIATION—Leaves are fundamentally undivided and have variable apices, the variation typically expressed on a single shoot (Fig. 33: 2, 3). The frequency of short bifid leaves varies and may be quite common, as in *Macmillan 73/493*.

NOTES ON TYPE SPECIMENS—1) *Lophocolea calcarea* Steph. The type, which was gathered on calcareus rock, is stated in the protologue to be in the Stephani herbarium.

Plants are pale brown. Trigones are variable and may be knot-like (on leaves of distal sectors of shoots) or medium to small (on leaves of median and basal sectors of shoots). Such smaller trigone size is atypical for the species and occurs in suboptimal material. Leaf apices are variable, as stated in the protologue, and rounded lobes frequently occur. Underleaves are free or weakly connate on 1 side (only the connate condition is noted in the protologue). The underleaf disc is entire or has a tooth or cilium on each side. Disc armature is not noted in the protologue, and only entire-margined underleaves are illustrated in the icone of the species (*Lophocolea* no. 160). Bract apices have 2 low, rounded lobes or are distinctly bifid by acute lobes. Perianths are trigonous. The specimen represents a somewhat weaker phase of *C. calcareus*.

A Colenso specimen labeled *Lophocolea calcarea* from WELT contains only a single shoot of cf. *Lamellocolea*.

2) *Lophocolea wairoae* Herzog. The specimen represents a small, suboptimal, perhaps subjuvenile phase of *C. calcareus*. Some shoots have underleaves bifid to ca. 0.5 and thus match the protologue, whereas the more developed shoots have underleaves bifid to ca. 0.6–0.8.

DISTRIBUTION AND ECOLOGY—The species is endemic to New Zealand (sea level–610 m), where it is restricted to calcareous sites. The plant is sporadic in distribution, and occurs in limestone caves, on shaded limestone rocks and cliff bases, as well as on exposed calcareous slopes and ledges. It may occur in disturbed sites, such as on calcareous soil under willows near a flour mill (Maheno, Otago Prov., leg. Child) or

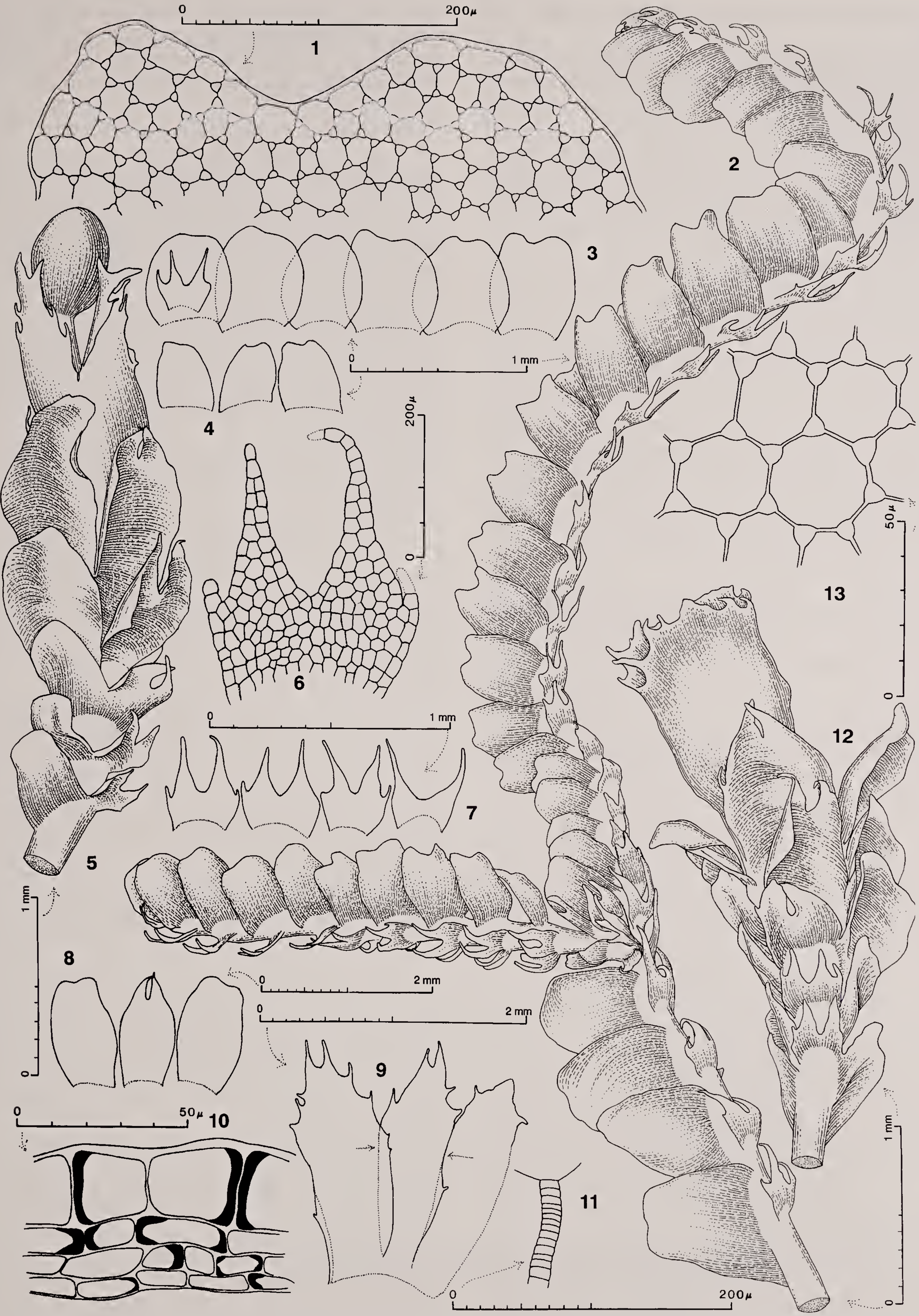

FIG. 33. *Chiloscyphus calcareus* (Steph.) J. J. Engel & R. M. Schust. **1.** Distal sector of leaf; note border of somewhat larger (especially longer) cells. **2.** Main shoot with lateral-intercalary branch, ventral-lateral view. **3.** Leaves and within at left, an underleaf, all from 1 shoot. **4.** Leaves. **5.** Gynoecium with mature sporophyte, ventral-lateral view. **6.** Underleaf. **7.** Underleaves from 1 shoot. **8.** ♀ Bracts and in middle, bracteole; note figure drawn at 0.5× magnification of leaves. **9.** Perianth, ventral lobe in middle. **10.** Capsule wall, cross section. **11.** Antheridium. **12.** Gynoecium, ventral view. **13.** Median leaf cells. (**1–3, 5–13,** from *Schuster 49545a*, New Zealand, North Is., Maungaraki Range; **4,** from *Macmillan 73/493* = New Zealand, South Is., Pleasant Point.)

on damp limestone walls in quarries (Kakanui, Otago Prov., leg. Child).

Specimens Seen—**NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Near Nightcaps, *Child H 1637* as *L. minor* (F). **OTAGO:** Kakanui, S of Oamaru, ca. 30 m, *Child H 1470* as *L. minor*–c. ♂ (F); Maheno, sea level, *Child H 135* as *L. minor*–c. per. + ♂ (F); near Weston, Oamaru, *Allison H 5703* as *L. minor* (CHR); Duntroon, *Allison H 6024* as *L. minor* (CHR); near Duntroon, *Allison H 5856* as *L. minor* (CHR). **CANTERBURY:** Pleasant Point, 185 m, *Macmillan 73/493* as *L. minor* (CHR); Castle Hill, ca. 610 m, *Child H 2066* as *L. minor* (F). **NORTH ISLAND. WELLINGTON:** Maungaraki Range, ca. 13 mi. S of Masterton, ca. 455 m, *Schuster 49545a*–c. sporo. + ♂ (F).

Sect. *Semiteres* J. J. Engel

Chiloscyphus Sect. *Semiteres* J. J. Engel, Novon 9: 22. 1999. Type: *Jungermannia semiteres* Lehm.

Branching terminal-lateral and lateral-intercalary or strictly lateral-intercalary. Leaves fundamentally undivided (occasionally short bifid in *C. rupicola*, but never consistently so); margins entire or (often in *C. rupicola*) dentate. Leaf cells with trigones mostly large to knot-like, occasionally medium and straight sided, exceptionally minute (some populations of *C. semiteres*). Underleaves 2–4-lobed at least to 0.5, at times divided nearly to the base; lamina margins on each side with a process grading from dentiform to lobuliform.

Asexual reproduction lacking.

Plants dioecious or paroecious. Androecia often forming elongate spikes; bracts slightly to distinctly smaller than leaves. Gynoecia variable in position: often on abbreviated lateral-intercalary branches lacking normal leaves, sometimes on terminal branches or main shoots. Capsule wall inner layer devoid of continuous sheets of pigmented thickening on vertical radial walls. Spore:elater diameter ratio 1.1–1.8:1.

The section is similar to the *Novaezeelandiae* but differs in the variable gynoecial position—some on short lateral-intercalary branches lacking vegetative leaves, others on main shoots, some on terminal branches. The sections also differ in sporophyte characters, sect. *Semiteres* having the seta composed of a greater number of cells in cross section, and the inner layer of the capsule wall lacking continuous sheets of wall material.

This pan-south temperate section is primarily Australasian in distribution. The section has three noteworthy disjunctions from the south temperate zone. The first involves *C. semiteres*, which is disjunct in the oceanic Isles of Scilly and Scotland. A second species, from Britain, probably also belongs here:

Chiloscyphus brookwoodianus **(Paton & Sheahan) J. J. Engel, comb. nov.**

Lophocolea brookwoodiana Paton & Sheahan, J. Bryol. 28: 163, f. 1, 2006. Type: Britain, Surrey, Brookwood Cemetery, *Sheahan* (E, *non vidi*), (see Paton and Sheahan, 2006).

The third is *Chiloscyphus platensis* (C. Massal.) J. J. Engel of NE Argentina and SE Brazil (see Grolle, 1985; Engel, 1998).

Key to the Australasian Species of Sect. *Semiteres*

1. Dorsal surface of leaves often hispid: at least some leaves on any given shoot armed with 1–3-celled teeth (the ventral surface smooth) . . . . [*C. gippslandicus*, see sect. *Hemispini*][4]

1. Dorsal (and ventral) surfaces of leaves uniformly smooth 2

  2. Plants dioecious; leaves without a border; perianth oblong to narrowly obovate, the lobes free for ca. 0.2–0.3 the perianth length 3

    3. Leaves with margins uniformly entire, the apices retuse to (*on weak or depauperate plants*) bidentate, the apices otherwise devoid of other armature; ♀ bract apices never retuse-bidentate to short bifid; oil-bodies (unknown for *C. fertilis*) 2–3(4) per cell, hyaline, glistening (except *C. canaliculatus*) 4

      4. Terminal branches present (varying from 30–90% in frequency); stems with cortical and medullary cell walls at most slightly thickened; perianth lobes distinctly bifid by acute to acuminate segments, the lobes otherwise dentate-laciniate; ♀ bracteole 0.6 or more bract area. Underleaves often 1.5–3× stem width. Pan-south temperate (widespread in Australasia) 5

        5. Underleaf disc lateral armature well-developed: mostly laciniate to lobulate; trigones minute to small, only occasionally medium and straight sided; underleaves often 1.5–3× stem width; plants translucent; oil-bodies hyaline and glistening, 2–3(4) per cell, mostly elliptic to fusiform; perianth lobes bifid . . . . *C. semiteres* (p. 91)

        5. Underleaf disc lateral armature reduced: mostly dentiform to ciliiform or lacking, only sporadically small-laciniiform; trigones normally large and bulging to knot-like (in shade forms medium and straight sided to weakly bulging); underleaves normally 1–1.5× stem width; plants dull-opaque; oil-bodies greyish orange, 3–7(9) per cell, nearly always spherical; perianth lobes undivided . . . . *C. canaliculatus* (p. 103)

      4. Terminal branches lacking, branching strictly lateral-intercalary; stems with cortical and medullary cell walls very thick; perianth lobes entire, or repand–sparsely denticulate, or with 1–2 of lobes short bifid, never with all 3 lobes bifid; ♀ bracteole 0.2–0.4 bract area. Underleaves 0.7–1.2× stem width; trigones knot-like. Australia (N.S.W.) . . . . *C. fertilis* (p. 107)

    3. Leaves (at least in some instances on any given shoot) armed with 1 or more coarse teeth; ♀ bract apices often retuse-bidentate to short bifid; oil-bodies 2–6(7) per cell, dull, opaque. Branching of sterile shoots normally all or nearly all lateral-intercalary (95–100%), terminal branching normally sporadic or lacking; trigones knot-like. New Zealand (North Is.), Tasmania . . . . *C. rupicola* (p. 110)

  2. Plants paroecious; leaves with a border of smaller cells; perianth clavate to subcampanulate, the lobes free for 0.5–0.6 the perianth length. Perianth lobes deeply bifid by acuminate to subcaudate segments. Australia (N.S.W.) . . . . *C. monoicus* (p. 115)

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[4] Surface teeth are nearly always present, but the character may be suboptimally expressed in sporadic populations. Careful search should be made of such sparsely armed variants before it is concluded that surface teeth are lacking (p. 189).

Chiloscyphus semiteres (Lehm.) Lehm. & Lindenb.

Jungermannia semiteres Lehm., Linnaea 4: 363. 1829. *Chiloscyphus semiteres* (Lehm.) Lehm. & Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hep. 190. 1845. *Lophocolea semiteres* (Lehm.) Mitt., J. Linn. Soc. Bot. 16: 188. 1877. Type: South Africa, Cape Prov., (Cap. Bonae Spei), "latere orientali montis Teufelsberg," *Ecklon* (G!).

Plants soft, prostrate, pale green to yellow green, translucent, fragrant; shoots usually to 2.2 mm wide (rarely 3.8–4 mm wide). Branches common, of lateral-intercalary and *Frullania* types, the two types varying in frequency but normally at least 30% of branches being terminal; half-leaf of terminal branches of same basic shape as the leaves. Stems rather narrow for plant size, 11–12 cells high, the cortex poorly differentiated, in 1–2 rows of slightly thick-walled cells; medullary cells thin walled. Rhizoids in an ill-defined zone from stem at base of underleaves. Leaves rather inflated in appearance, alternate, dorsally assurgent in basal portion, the distal portion broadly to sharply deflexed grading to subhorizontal throughout, occasionally with all or major portion of leaf subvertical to vertical; leaves widely spreading, loosely to densely imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip. Leaves with a broad adaxial concavity, oblate to asymmetrically and obtusely deltoid, well-developed leaves to 1.7× wider than long; apex undivided and normally entire, broadly rounded to truncate to occasionally retuse to (in weak or depauperate plants) sporadically bidentate to short bifid, the apex otherwise devoid of other armature; margins entire, the dorsal gradually and broadly curved, deflexed, at times sharply so, and forming a cnemis, short to rather long decurrent, the ventral more sharply curved than the dorsal margin, plane or occasionally somewhat deflexed. Leaf cells with walls thin, trigones minute to small, only occasionally medium and straight sided, 2.4–4.8 µm, the ratio of trigone diameter to length of intervening thin wall between trigones 1:2–5.6, with median leaf cells 28–31 µm wide, 25–35 µm long; surface smooth. Oil-bodies occupying small fraction of cell lumen, hyaline and glistening, 2–3(4) per cell, mostly coarsely botryoidal, the segments 1.3–2.6 µm, the oil-bodies subglobose, but more often grading to elliptic to fusiform, 9.1–11.1 × 5.9–6.5 µm, some 5.2–5.9 × 3.9–4.6 to 7.2 × 5.2 µm, subglobose ones 5.9 µm in diam.; oil-bodies of sporadic populations (*Engel 20164*) more finely segmented and smaller, being rather finely papillose and mostly 8.5–9.8 × 3.9–5.2 µm, with some 6.5–7.2 × 3.3 µm. Underleaves much smaller than leaves, highly variable in size, often 1.5–3× stem width (especially in well-developed plants), narrowly connate on 1 or both sides, insertion often asymmetric, the insertion crescent shaped, the underleaves appressed, distant to approximate, plane to slightly convex (ventral view), subrectangular to narrowly ovate; apex 2(4)-lobed to 0.6–0.8 or more by a variably shaped sinus, the lamina at times reduced and 4–5 cells high (sinus base to underleaf base); lobes ± parallel to strongly diverging, narrowly acute to acuminate, 5–12 cells wide at the base, the lobe margins entire or with a few teeth or cilia, particularly on the margin delimiting the sinus; lamina margins of well-developed shoots on each side with a process grading from laciniiform to lobuliform (the underleaves then 4-lobed), the lamina margins often with 1–2 accessory teeth or laciniae.

Asexual reproduction absent or, occasionally, by regeneration.

Plants dioecious. Androecia on main shoots or elongate, indeterminate *Frullania*- or lateral-intercalary–type branches, the androecia initially terminal but eventually become intercalary, the androecia then often composed of numerous (up to 20) bract pairs; androecia also on short, abbreviated lateral-intercalary branches that may or may not proliferate vegetatively distally; androecia of two ± intergrading types, the extremes being: 1) subfolious, the bracts foliaceous, of similar basic shape as vegetative leaves but slightly smaller, widely spreading, ventricose, and dorsally assurgent in basal portion, the distal portion soon becoming subhorizontal and slightly convex, the imbrication much as in leaves, the lobule small in proportion to bract size; and 2) spicate, the bracts much smaller than leaves, strongly dorsally assurgent and vertical, erect, appressed to bract immediately above, strongly ventricose-subcucullate, so much so that the dorsal pocket is rather ill-defined and large in proportion to bract size; bracts of both types with apices broadly rounded to truncate, the apices and margins entire. Lobule fused toward base with that of opposing bract, the free margin incurved, narrowly rounded, sometimes longer and then flap-like, crenulate, with slime papillae; antheridia 1 per bract, the stalk long, of 20–33 cells, uniseriate. ♂ Bracteoles often concave. Gynoecia dorsally assurgent, on main shoot or lateral-intercalary branches of variable length: often reduced, abbreviated and lacking normal vegetative leaves, less often longer and with a few to several cycles of normal leaves, or on rather short to long *Frullania*-type branches, rarely on ventral-intercalary branches; subfloral innovations absent. Bracts of innermost series larger than leaves, erect and ensheathing perianth, free from one another but in close proximity, concave in basal portion, ovate; apices often undulate, often canaliculate because of distally revolute margins, the apex rounded to ± truncate, with 1–2 (rarely more) low rounded projections or sharp teeth; margins often reflexed, entire or the ventral and sometimes also the dorsal margins with a few low rounded projections or sharp teeth. Bracteoles of innermost series considerably smaller than bracts, ca. 0.6 or more the bract area, narrowly to rather broadly connate on 1 or both sides, ± plane, narrowly ovate to subrectangular; apices bifid to ca. 0.3–0.5 by acuminate lobes; lamina margins entire or sparingly dentate and/or laciniate. Perianth occasionally produced, longly exserted beyond bracts, sharply trigonous throughout, the ventral side sometimes infolded, the perianths oblong to narrowly obovate, not or slightly expanding toward the wide, 3-lobed mouth; lobes shallowly bifid, the segments irregularly acute to acuminate, entire or with a few small teeth, the lobes otherwise dentate to laciniate; keels sharp, with keelar wings rare, of a few cells high. Calyptra large, extending to level of sinus base of perianth lobes.

Seta 9–11 cells in diam., with 30 rows of outer cells (with corners thickened as in medium-sized trigones) surrounding an inner core of scattered cells somewhat smaller than outer row. Capsule elliptic, 1100–1200 µm × 700–870 µm, the wall 43–48 µm thick, of 5–6 layers, the outer layer of cells equal to thickness of 2–2.2 of interior strata; outer layer of cells wide subrectangular, the radial walls thin, with magenta nodular to feebly spine-like thickenings mostly on longitudinal walls, those on transverse walls sporadic and smaller, the exposed tangential wall slightly thickened; intermediate and inner layer of cells subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended, sporadically becoming semiannular; innermost layer of cells irregularly short to long rectangular, the walls very thin, with semiannular bands red brown, rather common, narrow, often nonpigmented in median portion, often incomplete, sporadically forked, the radial walls often with nodular to spine-like thickenings.

Spores 9.6–11 µm, pale brown, thin, with faint, dense, low but sharply defined, close, papillose, and short-vermiculate markings, spore:elater diameter ratio 1.1–1.3:1. Elaters somewhat tortuous, 7.7–8.6(–9.6) µm wide, tapered to tips, the spirals 2.4–2.9 µm wide, loosely wound.

DIFFERENTIATION—*Chiloscyphus semiteres* may be recognized by the combination of: 1) undivided entire leaves with apices broadly rounded to truncate to retuse; 2) the often oblique insertion and orientation of underleaves (Fig. 34: 8); and 3) underleaves divided to 0.6–0.8. Well-developed plants also have leaves that are initially dorsally assurgent but then become reflexed distally, sometimes in the median portion of the leaf, sometimes only near the apex (Fig. 34: 9). The leaves are commonly deflexed along the dorsal margin (and then forming a cnemis) and at the apex; such plants bear a striking superficial resemblance to certain facies of the holarctic *Plagiochila asplenioides* (L.) Dumort. (see, e.g., fig. 550: 3 in Schuster, 1980).

Chiefly because of the plasticity of this species, confusion is quite possible with several other taxa. Sporadic collections (ex. *Engel 12868*) have leaves subvertical to vertical, and this feature, plus the adaxial leaf concavity, lend an appearance somewhat like that of *Clasmatocolea humilis*. Smaller plants with subvertical and adaxially concave leaves bring to mind *Clasmatocolea vermicularis*. In such plants (which are frequently male), underleaf characters should be studied with care—*C. vermicularis* has underleaves bifid to 0.3(0.5) and narrower than the stem. However, in both these *Clasmatocolea*-like facies, plants that grade to more typical *Chiloscyphus semiteres* are normally present, and care should be taken in searching for them. At times vertical-leaved phenotypes resemble *C. austrigenus* subsp. *okaritanus*, but the distinct underleaf differences will distinguish the two. Problems may arise with phases of subsp. *okaritanus* that have more deeply divided underleaves. Underleaves of such plants, however, are always bifid to less than 0.3, and underleaves more typical of subsp. *okaritanus* are usually present near the shoot apex.

Underleaves provide the chief characters to differentiate *C. semiteres* from *C. novaezeelandiae* (see Differentiation of the latter, p. 77). Underleaves of *C. novaezeelandiae* are concave, have disc margins on each side at most 1–3-dentate (only occasionally with one of the processes laciniiform), and tend to be more shallowly bifid (divided to 0.4–0.6, only rarely and sporadically to 0.7–0.8 and then never consistently so). Underleaves of *C. semiteres*, on the other hand, are convex,[5] often have a prominent laciniiform to lobuliform process on each side, and, on the whole, tend to be more deeply bifid. The underleaf sinus depth of *C. semiteres* is variable at the population level. Some populations have underleaves bifid to 0.6–0.75, others to 0.7–0.8 and with a lamina of only 4–5(6) cells high, whereas still other populations have underleaves deeply divided, many nearly to the base, with tissue between sinus base and underleaf base barely perceptible. Ecology is often a useful tool in treatment of these two species: *C. novaezeelandiae* usually occurs in the vicinity of moving water, whereas *C. semiteres* occurs primarily in more mesic or xeric sites.

Chiloscyphus semiteres has a characteristic appearance when dry. The leaves are subvertical to vertical, with the adaxial surfaces of opposing leaves connivent or nearly so. This orientation totally hides the stem in dorsal view. The leaf apices are sharply reflexed to revolute.

VARIATION—*Chiloscyphus semiteres* (in Australasia) and *Leptoscyphus expansus* (Lehm.) Grolle, an amphiatlantic species, share some interesting features. Both are weedy and polymorphic. Whereas *L. expansus* is one of the most common hepatics in southern South America, *C. semiteres* is likewise for Tasmania and, to a slightly lesser extent, New Zealand. Each occupies similar ecological niches, and because *L. expansus* is absent from Australasia, it would seem that *C. semiteres* replaces it there. To understand antipodal Lophocoleoids of both the American and New Zealand sectors, the many variants of both taxa must be understood. *Chiloscyphus semiteres* is treated here in considerable detail chiefly for this reason.

Well-developed *C. semiteres* should offer no problems—the leaves are obtusely deltoid, broader than long, dorsally assurgent, at least toward the base, a distinct cnemis is often present, and the apex and margins are devoid of teeth (see also under Differentiation). However, suboptimal plants may offer difficulties, in that some of them appear quite different from optimal phenotypes. For example, smaller phenotypes often have underleaves reduced in size, and with a short lamina subtending lanceolate lobes. However, this is not always the case—smaller phenotypes occasionally have underleaves consistently robust and appear outsized for the stature of the plant. Relative development of a cnemis is also variable. Leaves tend to lose the cnemis both in smaller phenotypes and in larger, more luxuriant but lax forms. In general, leaves have a cnemis if they are subvertical, or at least initially dorsally assurgent. Leaves that lack a cnemis generally are broadly and gently convex and are subhorizontal in orientation.

Very weak or depauperate plants, however, are the most problematic. Here the leaves are frequently longer than wide and ovate to subquadrate. Such plants tend to have leaf apices occasionally bidentate-retuse or less often short bifid. Because *C. rupicola* often has short bifid leaves, care should be exercised with suboptimal plants, and other characters, such as branching, should be checked. When well-developed plants of *C. semiteres* are at hand, the consistently undivided, entire leaves, both on main shoots and on branches, will separate this species from the allied *C. rupicola*.

Androecia are variable, and the extremes are quite different. The foliose type, characterized by number (1) in the species description, occurs on main shoots or leading branches (Fig. 35: 7). The spicate type, characterized by number (2) in the description, occurs on short, abbreviated, lateral-intercalary branches. Such branches either totally lack normal vegetative leaves or produce them only distal to androecia, i.e., never at the branch base (Fig. 35: 6). Androecia somewhat intermediate between these extremes are shown in Fig. 35: 1.

Hässel de Menéndez (2000) narrowed the circumscription of *Chiloscyphus semiteres* by excluding the southern South American population and treating that as *C. aequifolius* (Nees & Mont.) Hässel. Also, the synonyms of *C. semiteres* on the

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[5] Care should be taken here to be certain that shoots are strictly vegetative, in that ♂ bracteoles are often concave.

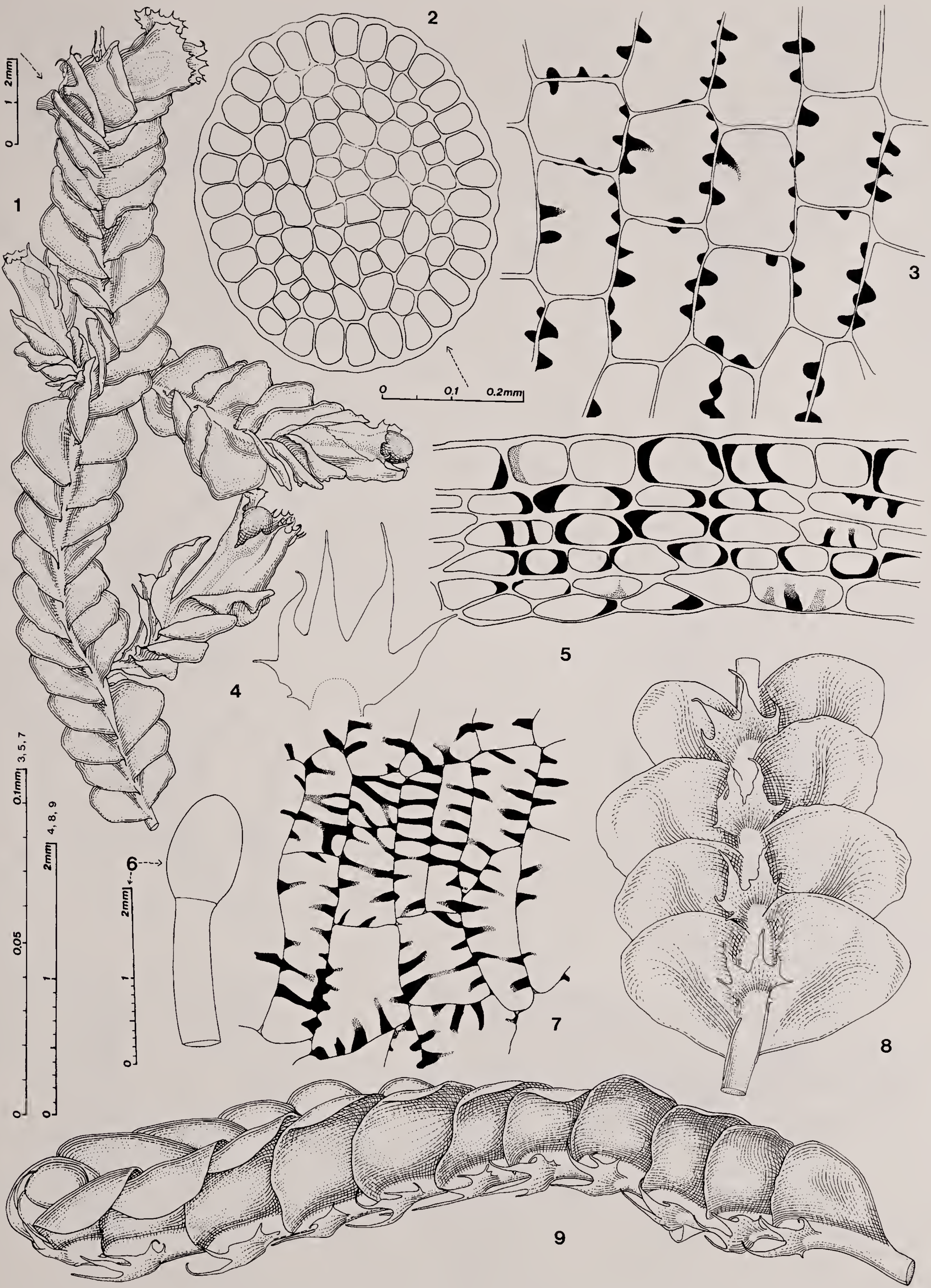

FIG. 34. *Chiloscyphus semiteres* (Lehm.) Lehm. & Lindenb. (All var. *semiteres*). **1.** Shoot, with 4 mature sporophytes on gynoecial axes of varying lengths (note: main shoot leaf associated with lowermost branch is removed to show branch base). **2.** Seta, cross section. **3.** Capsule wall, outer layer. **4.** Underleaf. **5.** Capsule wall, cross section. **6.** Capsule profile. **7.** Capsule wall, inner layer. **8.** Shoot, ventral view. **9.** Shoot, lateral view. (**1–3, 5–9,** from *Engel 19882*, Tasmania, Tahune Forest Reserve; **4,** from *Norris 27222*, Tasmania, near Devil's Gate Dam.)

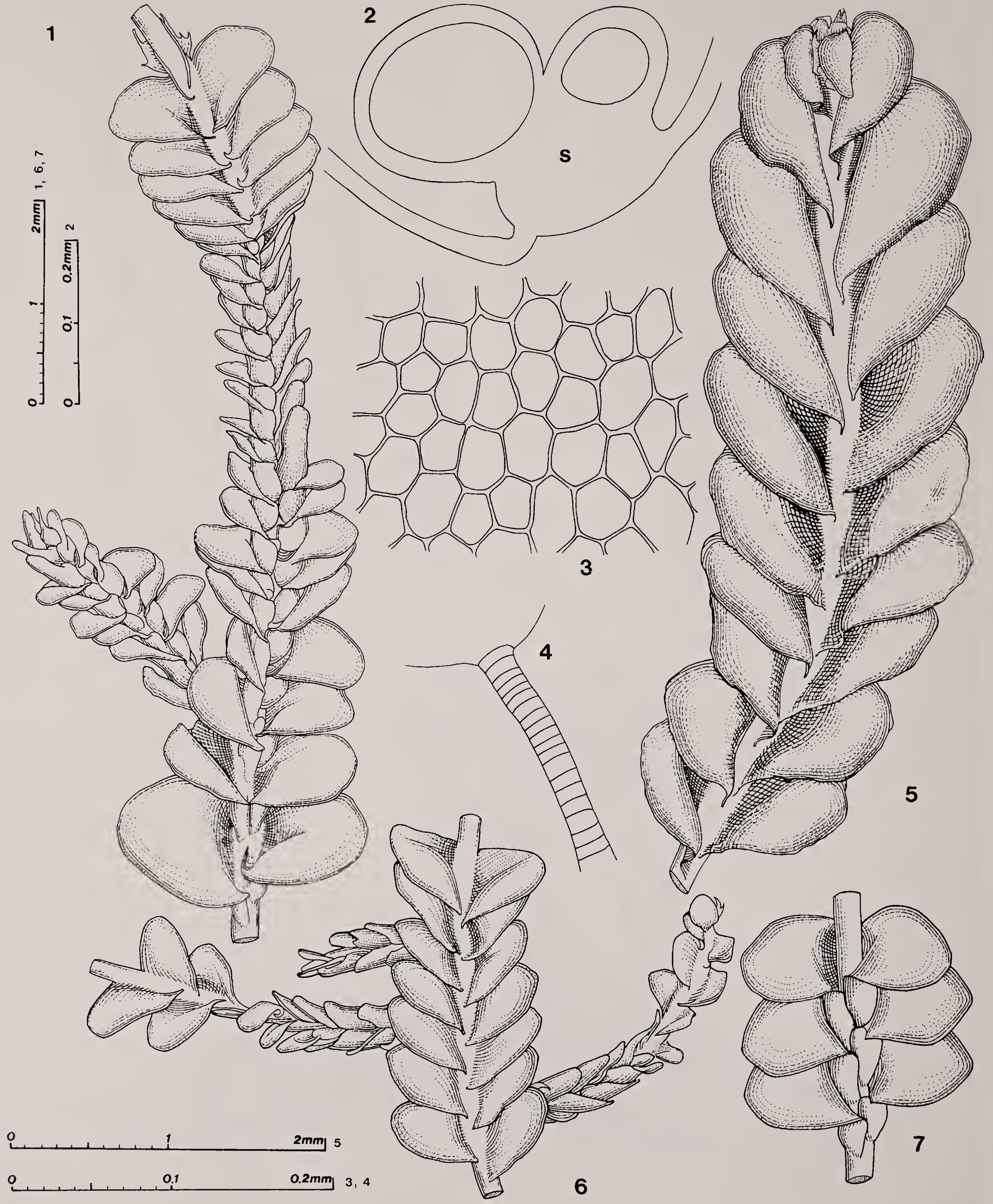

FIG. 35. *Chiloscyphus semiteres* (Lehm.) Lehm. & Lindenb. (All from var. *semiteres*). **1.** Androecium-bearing main shoot and branch. **2.** Opposing antheridial bracts with stem (= s), cross section. **3.** Median leaf cells. **4.** Antheridial stalk. **5.** Shoot, dorsal view. **6.** Shoot with 3 spicate androecia. **7.** Portion of foliose androecium (note flaps on 2 lower right-hand lobules). (All from *Engel 19882*, Tasmania, Tahune Forest Reserve.)

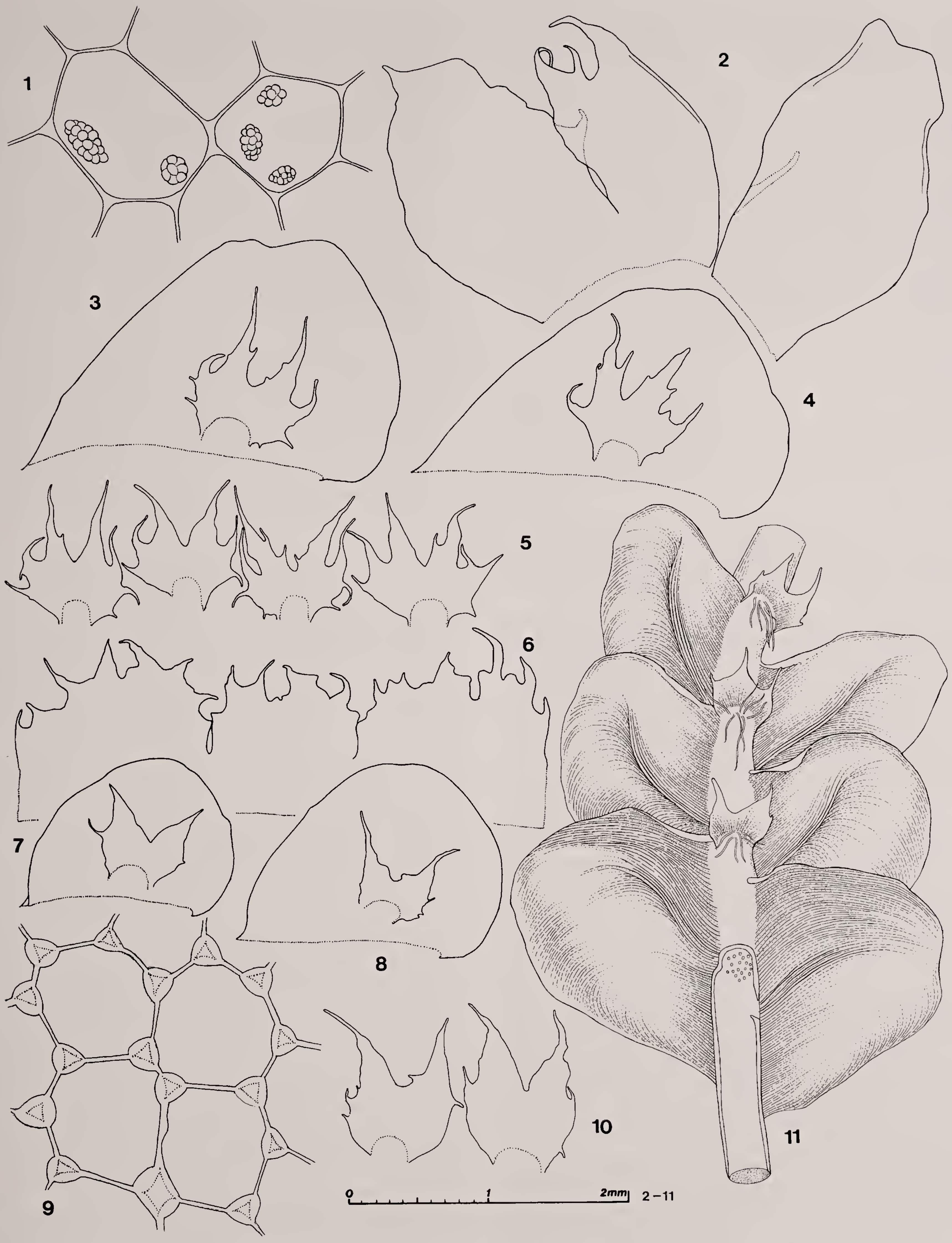

FIG. 36. *Chiloscyphus semiteres* (Lehm.) Lehm. & Lindenb. (**1–6**), and *Chiloscyphus canaliculatus* Gottsche, Lindenb. & Nees (**7–11**). **1.** Median leaf cells with oil-bodies (857×). **2.** Innermost ♀ bracts and in middle, bracteole. **3, 4, 7, 8.** Leaves and within, underleaves. **5.** Underleaves from one shoot; note variation, including (left to right) increase in stature of lateral armature culminating in feeble 4-lobed condition. **6.** Perianth mouth, ventral lobe in middle. **9.** Median leaf cells. **10.** Underleaves from 1 shoot. **11.** Sector of shoot, ventral view. (**1–4, 6,** from *Engel 19882*, Tasmania, Tahune Forest Reserve; **5,** from *Engel 19883*, same loc.; **7, 8,** from *Engel 13013*, Tasmania, Victoria Valley Falls; **9,** from *Engel 20096*, Tasmania, Zeehan-Renison Bell State Reserve; **10,** from *Engel 20187*, Tasmania, Mt. Wellington, off Pipeline Track; **11,** from *Engel 14169*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park, Hugel River, just W of Watersmeet.)

basis of southern South American plants were moved by Hässel de Menéndez (2000) to the synonymy of *C. aequifolius*. Hässel de Menéndez (2000) stated that the southern South American species developed microcladia or regenerants, whereas *C. semiteres*, in the strict sense, did not. Hässel de Menéndez (2000), however, was unable to demonstrate presence of regenerants in type material of *C. aequifolius*.

Hässel de Menéndez (2000) studied type plants *C. semiteres* and stated (p. 252) that "the yellowish color, the smaller leaf cells and the leaf insertion and position, as well as the narrower amphigastria segments, are different from those of *Chiloscyphus aequifolius*." Hässel de Menéndez (2000, p. 254) stated that *C. aequifolius* differed from *C. semiteres* "because it has entire as well as bifid leaves," and that "if trigones are present [in *C. aequifolius*], they are smaller than in *C. semiteres*." These purported differentiating characters are each discussed below.

Comments that follow are based on study of hundreds of specimens of *C. semiteres* over a broad geographical range. Populations of *C. semiteres* over a broad range in Australasia (i.e., the range encompassed in this treatment) are used for comparison to populations from southern South America and South Africa.

- Australasian plants are pale green to yellow green and not different from the "plane green, yellowish when dry" (Hässel de Menéndez, 2000, p. 247) color as described for *C. aequifolius*.
- Australasian plants have median leaf cells that are 28–31 µm wide × 25–35 µm long, which is a range rather similar to the (23)28–35 µm wide × 23–40 µm long cell size range stated for *C. aequifolius* (Hässel de Menéndez, 2000).
- Australasian plants have the orientation and insertion of the leaves strongly succubous, with the insertion lines extending to the stem midline dorsally and thus not defining a leaf-free strip of stem cells, and are not recurved at the ventral end. Hässel de Menéndez (2000, p. 247) stated that *C. aequifolius* has long-oblique leaf insertion lines that do not extend to the stem midline dorsally and define a leaf-free strip of 1–2 cells, and that ventrally "an inverted U arch [is] reduced or non existent" (see Hässel de Menéndez, 2000, fig. 1: 5, 6), the latter character thus not different from Australasian populations. I have studied leaf insertion lines in populations from Australasia, South Africa, and southern Chile, and all are similar in extending to the stem midline dorsally. The extreme dorsal base of "opposing" leaves may be inserted at the midpoint of cells lying juxtaposed on each side of the stem, but no row of leaf-free cells is present. It should be noted that the leaf insertion lines appear to extend to the stem midline dorsally in several of Hässel's habit illustrations of *C. aequifolius* (e.g., Hässel de Menéndez, 2000, fig. 1: 1, 2; 3: 1).
- Hässel de Menéndez (2000, p. 252) stated that the underleaf lobes (segments) of the type of *C. semiteres* were 6–8 cells wide at the base and were narrower than those of *C. aequifolius*, which she found to be 10–12 cells wide at the base. Note that the illustration of the underleaf of *C. aequifolius* by Hässel de Menéndez (2000, fig. 3: 8) has both of the underleaf lobes 8 cells wide at the base. I have found variability in magnitude of underleaf lobes and lamina armature in *C. semiteres*, and I am unable to make these distinctions. For example, New Zealand populations have underleaf lobes 5–12 cells wide at the base, whereas those from southern South America (+ Juan Fernandez) have underleaf lobes 5–8 cells wide at the base.
- Hässel de Menéndez (2000, p. 254) stated that *C. aequifolius* has undivided as well as bifid leaves, a character that differentiated the species from *C. semiteres*. The description of the leaves of *C. aequifolius* in Hässel de Menéndez (2000, p. 247) referred to them as "ovate to rectangular truncate, entire, ... or some branches with bifid leaves." In my experience, the leaf apex of *C. semiteres* may be occasionally retuse and, in weak or depauperate plants, grade to sporadically bidentate to short bifid. It is notable that no bifid leaves are illustrated for *C. aequifolius* in Hässel de Menéndez (2000).
- Hässel de Menéndez (2000) found that trigones present in *C. aequifolius* are smaller than in *C. semiteres*. I have spent many hours studying the magnitude of trigones of *C. semiteres*, especially in connection with differentiation of the species from *C. canaliculatus*. Trigones of *C. semiteres* are minute to small and only occasionally are medium and straight sided; I have seen many populations of *C. semiteres* with trigone size similar to those shown in Hässel de Menéndez (2000, fig. 3: 5, 6). (Also see Note 1 below.)

In view of the lack of characters differentiating the southern South American population, and after this re-evaluation process, I am here treating *C. semiteres* in the sense of Grolle (1959) and Engel (1990a).

NOTES—1) The trigone character should be checked by examination of leaves from several different shoots. This is particularly necessary in populations with medium and straight-sided to slightly bulging trigones because different shoots often have trigones of somewhat different magnitude.

2) Rudimentary androecia are frequent in this species. In such cases, the leaves have a small rudimentary dorsal pocket or merely have the insertion curved apically at the dorsal end (see leaves toward top of Fig. 35: 1). Also, opposing leaves are frequently connate dorsally. Rudimentary bracts may occur basal or distal to functional male bracts, or entire shoots may have them. Such rudimentary bracts are nonfunctional, in that they have not been found associated with antheridia.

3) The position of vegetative and sexual lateral-intercalary branches is somewhat variable. Branches mostly originate near the juncture of an underleaf and the ventral base of the adjacent leaf, or at times they originate from the ventral-lateral side of the stem. Branches less often are lateral and approximately midway between the ventral bases of two leaves. In very rare cases (only one collection seen, *Schuster 67-3882*), some branches occur between the ventral end of the leaf and the underleaf insertion, whereas others are in the lateral half of an underleaf axil. True ventral-intercalary branches (from the median sector of an underleaf axil) are lacking, which contradicts Grolle (1959, p. 591).

4) Many perianths contain two calyptrae: one associated with a fully developed sporophyte and nearly as long as the perianth, the other reduced and extending to ca. 0.5 the perianth length.

5) Occasionally dorsal surfaces of leaves have scattered colonies of the alga *Chlorosaccus fluidus* Luther (Heterokontae, Heterocapsales; det. P. Ponce). Leaves with such algae appear as if submuricate under the dissecting microscope.

Examination under the light microscope will immediately clear up any possible confusion with muricate-leaved taxa.

DISTRIBUTION AND ECOLOGY—The species is one of the most xeric tolerant of Australasian leafy hepatics. It is very common in drier sectors of Australia and New Zealand, and in Tasmania and Australia it is one of the most common or perhaps the most common hepatic. The species for the most part is intolerant of high moisture levels: it is rare in the western sectors of southern South Is., New Zealand, as well as western and southwestern Tasmania.

The species has a broad ecological amplitude. For example, in New Zealand it may occur in wet, rich, mixed *Nothofagus* forests along the Tutoko River in Fiordland Natl. Park, as well as on sandy ground of the St. Kilda Golf Course near Dunedin. A similar range exists for Tasmania: it occurs in wet forests consisting of *Nothofagus cunninghamii*, *Eucalyptus*, *Atherosperma*, *Pomaderris apetala*, and *Phyllocladus* along the Huon River in the Tahune Forest Reserve, but also at the edge of an open *Casuarina* pine forest in Asbestos Range Natl. Park (a dry site with few other bryophytes present).

Further comments on distribution are placed under each of the varieties.

Chiloscyphus semiteres is divisible into two varieties that are separable as follows.

Key to Varieties of *C. semiteres*

1. Leaf apices (weak or depauperate plants excepted) undivided to occasionally retuse. Broadly distributed in Australasia . . . . var. *semiteres*
1. Leaf apices often retuse-short bifid, the lobes usually rounded. Australia . . . . var. *retusus*

Chiloscyphus semiteres (Lehm.) Lehm. & Lindenb. **var. *semiteres***

Jungermannia heterophylla var. *simplex* Lehm., Linnaea 4: 363. 1829, *syn. fide* Gottsche, Lindenberg & Nees (1845). *Lophocolea heterophylla* var. ß *simplex* (Lehm.) Gottsche, Lindenb. & Nees, Syn. Hep. 157. 1845. Lectotype (*fide* Grolle, 1976): South Africa, Cape Prov., E side of Table Mtn., *Ecklon* (W, *non vidi*); possible isolectotype: (BM!).

Jungermannia bridelii Lehm. & Lindenb. *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. 4: 45. 1832, *syn. nov. Lophocolea bridelii* (Lehm. & Lindenb.) Nees *in* Gottsche, Lindenb. & Nees., Syn. Hep. 157. 1845. *Chiloscyphus bridelii* (Lehm. & Lindenb.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 412. 1985 (1984). Type: Australia, sin. loc., *Labillardiére*, "Herbarium Lehmannianum" (S!–c. ♂).

Lophocolea aequifolia Nees & Mont., Ann. Sci. Nat. Bot. II. 5: 55. 1836, *syn. fide* Grolle (1959). *Chiloscyphus aequifolius* (Nees & Mont.) Hässel, J. Hattori Bot. Lab. 88: 245, 2000. Type: Juan Fernández Is., Apr. 1830, *Bertero 1598* (PC!, STR!).

Lophocolea heterophylloides Nees *in* Gottsche, Lindenb. & Nees, Syn. Hep. 157. 1845, *syn. fide* Grolle (1959). Lectotype (*nov.*): Australia (Nova Hollandia), without specific loc., *sin. coll.* [Sieber] *54* (STR!–c. per.).

Chiloscyphus lindenbergianus Nees *in* Gottsche, Lindenb. & Nees, Syn. Hep. 187. 1845, *syn. fide* Grolle (1959). Type: South Africa, "in latere septentrionali montis tabularis Promontorii Bonae Spei ... ," *Drege* (G!, STR!).

Lophocolea undulata Mont., Ann. Sci. Nat. Bot. Ser. III. 4: 351. 1845, *syn. fide* Grolle (1959). Lectotype (*nov.*): "*Chile australiori reperit cl. Gay. Herb. Mus. Par.*," *Gay s.n.* (PC!–c. young ♀); isolectotype: (W!, Lindenberg Hep. no. 4267–c. young ♀).

Chiloscyphus marginatus Colenso, Trans. & Proc. New Zealand Inst. 21: 60. 1889 (1888) ("*marginata*"), *syn. cf.* Stephani (1892). Lectotype (*nov.*): New Zealand, [Taupo], *Colenso a. 1311* (BM!); isolectotype: (WELT! sub *Colenso a. 1310*).

Lophocolea krauseana Steph., Bull. Herb. Boissier II, 6(8): 658. 1906 (= Spec. Hep. 3: 74), *syn. fide* Grolle (1959). Neotype (Hässel de Menéndez, 2000): Chile, Prov. Valdivia, Valdivia, *Hahn* (G!–c. per.).

Lophocolea dalliana Steph., Bull. Herb. Boissier II, 6(9): 785. 1906 (= Spec. Hep. 3: 85), *syn. fide* Grolle (1959). Type: New Zealand, without specific locality, *Dall s.n.* (G!–c. young ♀).

Lophocolea geheebii Steph., Bull. Herb. Boissier 6(9): 787. 1906 (= Spec. Hep. 3: 87), *syn. nov. Chiloscyphus geheebii* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 415. 1985 (1984). Type: Australia, Genoa River, 5000 ft., Feb. 1889, *Bäuerlen 169* (ex hb. Melbourne) (G!).

Lophocolea forsythiana Steph., Bull. Herb. Boissier 6(9): 788. 1906 (= Spec. Hep. 3: 88), *syn. nov. Chiloscyphus forsythianus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 415. 1985 (1984). Type: Australia, New South Wales, Turramurra, 14 Aug. 1898, *Forsyth 47* (G!–c. ♂, NSW!–c. ♂).

Lophocolea fernandeziensis Steph., Kongl. Svenska Vetenskapsakad. Handl. 46(9): 44. *f. 16 f, g.* 1911, *syn. fide* Grolle (1959). Type: Juan Fernández Is., Más a Tierra, Valle Colonial, 1908, *Skottsberg 55* (G!–c. ♂).

Lophocolea heterophylloides var. *crassiflora* Pearson, Univ. Calif. Publ. Bot. 10: 375. *pl. 105.* 1923, *syn. nov.* Holotype: New Zealand, North Is., Taupo, May 1904, *Setchell 49* (UC!–c. per. + ♂).

Lophocolea heterophylloides var. *decurrens* Pearson, Bull. Misc. Inform. 1924: 68. *fig. 1.* 1924, *syn. nov.* Holotype: Tasmania, New Norfolk, Swamp Road, Lachlan, 6 Nov. 1906, *Weymouth 1490* (BM!); isotypes: (F!, HO!).

Lophocolea krauseana var. *dissecta* Herzog, Arch. Esc. Farm. Fac. Ci. Med. Córdoba 7: 14. 1938, *syn. fide* Hässel de Menéndez (2000). Type: Chile, Concepción, Dep. Arauco, Laraquete, *Hosseus 736* (*non vide*).

Lophocolea calbucensis Herzog *in* Herzog, Schwabe & Schwabe, Beih. Bot. Centralbl. 60(B): 6. *f. 3.* 1939, *syn. fide* Grolle (1959). Holotype: Chile, Prov. Llanquihue, Calbuco, Ostrand, *Schwabe 26* (JE!–c. young ♀).

Lophocolea magnistipula S. W. Arnell, Rev. Bryol. Lichénol. 23: 175. *f. 2.* 1954, *syn. fide* Grolle (1959). Type: South Africa, Cape Prov., Kasteel Poort, *S. Arnell 1101* (BOL!, S!, UPS!).

Lophocolea squamata Herzog, Trans. Brit. Bryol. Soc. 1: 183. *f. 2c–i.* 1949, *syn. nov.* Holotype: Australia, Western Australia, Pemberton, April 1946, *G. G. Smith 78* (hb. Banwell, *non vidi*); isotype: (UWA!).

Leaf apices (weak or depauperate plants excepted) undivided to occasionally retuse.

DIFFERENTIATION—This species, *C. canaliculatus*, and *C. rupicola* have complex interrelationships. Superimposed on this complexity, and a contributory factor to that complexity, is the considerable variation involved with each of the three taxa. Table 9 illustrates these interrelationships and documents some of the variability.

Branching modalities are an integral part of the complexity of interrelationships involving *C. semiteres* and allies. As Table 10 illustrates, at times a strong correlation occurs between branch type and substrate, but in other instances the association is less positive. For example, *C. rupicola*, which is nearly always on wood, has all or nearly all branches of the lateral-intercalary type (see Table 10). On the other hand, branching patterns in *C. semiteres* are more plastic (Table 10). Terminal branching in that species is 1) abundant in terricolous populations (ex. *Engel 13612*); 2) predominant in populations on logs, accounting for two-thirds of branch types; and 3) somewhat reduced in saxicolous plants, varying from 28–46% of branch types.

NOTES ON TYPE SPECIMENS—1) *Jungermannia semiteres* Lehm. Specimens consist of rather flaccid shoots, some of which bear androecia. Leaf apices are for the most part broadly rounded to truncate, but occasionally are retuse.

TABLE 9. Comparative characteristics between *Chiloscyphus semiteres*, *C. canaliculatus* and *C. rupicola*. LIB = lateral-intercalary branch; F = *Frullania*-type branch.

Character	*C. semiteres*	*C. canaliculatus*	*C. rupicola*
Leaf armature	normally entire, the apex bidentate in suboptimal plants	entire	coarsely dentate
Underleaf lateral armature	small to large laciniiform to lobulate, sporadically tooth-like to small laciniiform	reduced: mostly tooth-like to cilia-like or lacking, sporadically small laciniiform	dentiform to laciniiform to sporadically lobuliform
Trigones	mostly minute to small and concave sided, occasionally medium and straight sided to sporadically feebly bulging	normally large and bulging to knot-like, occasionally medium to large, the sides straight to feebly bulging (shade plants)	knot-like, occasionally large in volume but sides straight to somewhat bulging
Trigone diameter (µm)	2.4–4.8	(4.8)6–7.2(8.4)	6–8.4(9.6)
Ratio of trigone diameter to length of intervening thin wall between trigones	1:2–5.6	variable: 1:(0.9)1.2–2.6(3.2)	1:0.7–2(2.8)
Branching (see Table 10)	F = 66–90% LIB = 10–34%	F = 28–46% LIB = 54–72%	F = 0–5% LIB = 95–100%
Oil-bodies	2–3(4) per cell, hyaline and glistening	3–7(9), light brown	2–6(7) per cell, dull, opaque
Texture	translucent	mostly dull–opaque	dull opaque
Substrate (Tasmania)	terricolous; boulders; rotted, sometimes bryophyte-covered logs; tree branches	terricolous; rocks; boulders	nearly always on wood of logs or upright trees

Underleaves are deeply divided, ca. 1.5–2× the stem width, and have lamina margins on each side with a conspicuous laciniiform to lobuliform process. Trigones are small to medium and straight sided.

2) *Jungermannia heterophylla* var. *simplex* Lehm. The specimen at BM is small and consists of only a few shoots. The leaves are strongly dorsally assurgent, the apices often retuse, the trigones small and the underleaves have a conspicuous lacinia on each side of the lamina.

3) *Jungermannia bridelii* Lehm. & Lindenb. I was able to locate only a single packet, containing a single shoot, of original material; that specimen, at S, is labeled "*Lophocolea Bridelii* Nobis, Syn. Hep. p. 157, Nov. Hollandia, *La Billardiere*, Herbarium Lehmannianum." Leaf cell trigones are lacking and the underleaf disc on each side has a well-developed laciniiform process. The specimen, which has an intercalary androecium, represents a rather well-developed phase of *C. semiteres*.

TABLE 10. Comparison of correlations of branch type and substrate between *Chiloscyphus semiteres*, *C. canaliculatus*, and *C. rupicola*.

Name	Engel collection no.	Branch type frequency[1] (%)	Substrate
C. semiteres	12989	F = 66 LIB = 34	fallen *Acacia* log
	19883	F = 66 LIB = 34	bryophyte-covered decorticated log
	13612	F = 90 LIB = 10	gravely soil
C. canaliculatus	12688	F = 46 LIB = 54	thin soil layer over boulder
	14471	F = 30 LIB = 70	soil over rock adjacent to huge boulder
	20187	F = 28 LIB = 72	rock in forest
C. rupicola	13626	F = 0 LIB = 100	dead tree base
	19762	F = 4 LIB = 96	bryophyte-covered large log
	20096	F = 5 LIB = 95	very rotted, crumbly, decorticated wood

[1] LIB = lateral-intercalary branch; F = Frullania-type branch. Percentages are based on examination of 50 branches from each collection number.

The specimen agrees quite well with the protologue, yet there are some concerns. First, although the label bears *Labillardiére* as collector, the protologue makes no reference to collector. Second, label data includes no indication of the Bridel herbarium, which was noted in the protologue. These concerns do not preclude this specimen as constituting at least part of the original material, and I provisionally assign type status to the collection. Original material is not at FI, H, HO, L, NSW, or PC; Bridel, Lehmann, or the materials of both are known to be deposited at several of these institutions.

4) *Lophocolea aequifolia* Nees & Mont. The underleaf lamina has on each side a dentiform to large laciniiform process. Trigones are small and concave sided to medium and straight sided. Leaf apices are broadly rounded to truncate to feebly retuse. The specimen represents a somewhat small, suboptimal phase of *C. semiteres*.

5) *Lophocolea heterophylloides* Nees. Three collections, all from Nova Hollandia (Australia), are cited in the protologue: a) Sieber no. 54 (with perianths), b) Sieber no. 47 (sterile), and c) Drummond (sterile). I have seen two Sieber collections from S (both sterile and lacking a number), each consisting of a few stems. Leaves are broadly rounded (upper sector of shoots) to retuse to 1-lobed to short bilobed (in lower sectors); the underleaf lamina on each side has a well-developed laciniiform process; trigones are small. The collections appear to be segregates of the same specimen (? no. 47), representing a somewhat suboptimal phase of *C. semiteres*. A specimen from STR lacks collector name but bears the number 54. The packet face has notes on the perianth and leaf–underleaf connation that agree with the protologue. The packet contains careful dissections of bract + bracteole, perianth and leaf + underleaf, all preserved between two small pieces of clear plastic and labeled. Details of these dissections agree with the protologue.

The packet also contains several shoots, some bearing perianths. Leaves are broadly rounded to (often) retuse to short bifid. The underleaf lamina has on each side a small to large laciniiform process; underleaves are connate on one or both sides. Trigones are absent or small. Some shoots have rather loosely imbricate leaves with apices mostly retuse to short bifid and underleaves narrowly connate on 1 side. Other shoots have more closely imbricate leaves that are mostly broadly rounded at the apex; these shoots have underleaves often connate on both sides and on one side may be distinctly so. Perhaps Nees had such a shoot at hand when describing a broad leaf–underleaf connation. The STR collection is designated the lectotype of *L. heterophylloides*.

6) *Chiloscyphus lindenbergianus* Nees. Nees included the following information in the protologue: "In latere septentrionali montis tabularis Promontorii Bonae Spei ad arborum cortices (Drege in Hb. L(ehmann)." I have seen four specimens, as follows. a) STR collection labeled *Chiloscyphus lindenbergianus*, "in latere septentr. montis tabularis C. b. sp. in cortice, Herb. Lehm." The specimen is scrappy and consists of two components: 1) *Clasmatocolea vermicularis* (orbicular leaves and short bifid underleaves narrower than the stem) and 2) one male shoot of *Chiloscyphus semiteres* (ovate leaves and rather deeply divided underleaves with a process on each side of the lamina). b) S collection labeled *Chiloscyphus lindenbergii*, "Cap b. Spei, *Drege*, Herbarium Lehmannianianus." The specimen consists of a small piece of bark with a few shoots of *Clasmatocolea vermicularis*. c) S collection labeled *Chiloscyphus lindenbergii*, "Synop. p. 187. no. 30, Tafelberg, Herbarium Lehmannianum." The specimen, without collector, is similar to (b) above and likewise is *Clasmatocolea vermicularis*. d) G collection labeled *Chiloscyphus lindenbergii*, "Promont. Bonae Spei, in Monte Tabulari;" the specimen lacks a collector but is marked "original." Leaves are ovate and often feebly retuse at the apex. Underleaves are bifid nearly to the base and the abbreviated lamina has on each side a narrow, long, laciniiform process. Trigones are lacking. Such leaves and underleaves are shown by Stephani in his icone of the species (*Chiloscyphus*, no. 9); the figure is based on a Drege specimen from "Cap bon spei, in Mt. Tabulari," with the added note "Original ex hb. Ldbg. Vindobon." A shoot of *Clasmatocolea vermicularis* is also present.

It appears that all of the above collections are segregate fragments of the same, original specimen, which contained two elements: one a weak phase of *Chiloscyphus semiteres*, the other *Clasmatocolea vermicularis*. It also appears that Nees used a combination of these two elements in the protologue. The orbicular leaf shape is found only in *C. vermicularis* and not in the *Chiloscyphus semiteres* element. On the other hand, the "repando-subretusis" character given to the leaf occurs in the *Chiloscyphus* element and not in *Clasmatocolea*.

The name *Chiloscyphus lindenbergianus* should be typified with the *Chiloscyphus* element because underleaf protologue data unambiguously matches only the *Chiloscyphus*. I do not wish to select a lectotype based only on the above specimens.

Stephani (1898–1924 [1907]) treated this species and erroneously spells the name "*Lindenbergii*."

7) *Lophocolea undulata* Mont. The specimen, which represents a rather well-developed phase of *C. semiteres*, possesses androecia and very young gynoecia (perianths barely discernable). Underleaves are only ca. 1.2–1.5× the stem width, and the lamina on each side has a small to medium laciniiform process and, often, 1–2 accessory teeth. Trigones are minute to small. The specimen at PC consists of numerous shoots; that at W is a fragment.

8) *Chiloscyphus marginatus* Colenso. I have seen material from BM, G, and WELT; material was not located at Y. The BM packet contains two elements with undivided, entire leaves; typification is therefore essential.

The first element consists of sterile, pale brown shoots and leaves with distinctly knot-like trigones (at least the trigones are pigmented). Leaf insertions do not reach the stem midline dorsally, and a leaf-free strip of 1–3 cells wide is delimited. Underleaves are narrowly connate on 1 or both sides, and the disc on each side has a dentiform to small laciniiform process. I provisionally assign these plants to *Leptoscyphus*. The Geneva specimen consists of two shoots that correspond to this element.

The second element more closely agrees with the protologue than the *Leptoscyphus* element. Plants of the second element have a prominent laciniiform to small lobuliform process on each side of the underleaf disc. That feature is a better match than the *Leptoscyphus* element to the protologue description of "two long laciniate flexuous teeth on each outside base." The leaf insertions of element two attain the stem midline dorsally; that character better fits the protologue than the *Leptoscyphus*. The protologue states that the leaves are decurrent and "with their extreme ends overpassing." Also, the leaves of element two may be deltoid, a shape mentioned in the protologue; that leaf shape does not occur in the *Leptoscyphus*. Lastly, the protologue states that plants are "pale," a feature that is better applied to the *Chiloscyphus* element than the *Leptoscyphus*. Element two corresponds to *Chiloscyphus semiteres*.

The *Chiloscyphus* element corresponds to a greater extent to the protologue, and I therefore designate that element of the BM specimen as lectotype of *C. marginatus*.

The WELT collection consists of four shoots, all fragmentary, flaccid, and all *C. semiteres*. They appear to be part of the BM specimen, but bear a different number—*a. 1310*.

Stephani (1892) placed *C. marginatus* as a synonym of *L. heterophylloides*. Hodgson (1943, p. 51) indicated that she did not see the plant, and *C. marginatus* is not mentioned in Hodgson (1953).

9) *Lophocolea krauseana* Steph. The specimen is a somewhat weak phase of *C. semiteres*, being rather small and having leaf apices occasionally retuse to retuse-1-dentate to short bifid. Underleaves are ca. 1.5–1.8× the stem width, and the lamina on each side has a rather large lacinium and, often, an accessory tooth or lacinia. Trigones are small and concave sided. Some perianths are barely exserted, as noted by Stephani in the protologue, others are distinctly exserted. The brown color noted by Stephani is likely due to improper drying when collected.

Stephani, in both the protologue and icon of this species (*Lophocolea* 74), stated that the collection was made by Krause in Corral, Chile. However, the specimen of *L. krauseana* from G (G 17817) is a Hahn collection from Valdivia. That collection also bears the word "Original" in Stephani script and has the orange "TYPUS" sticker affixed to the packet face. A second curiosity exists. Stephani, in his icon of the species, apparently illustrated a leaf from the basal sector of a shoot, in that it is "emarginato-bidentula," thus matching the protologue description of such leaves. Leaves more typical of the specimen are those Stephani stated occur in upper sectors of a shoot, i.e., "retusa vel obtusa vel late rotundata." Hässel de Menéndez (2000) selected the Hahn specimen from Valdivia (G 17817) as a neotype.

10) *Lophocolea dalliana* Steph. Plants are 3.8–4 mm wide and therefore exceptionally large for *C. semiteres*. Underleaves are 0.6–0.8-fid, ca. 1.5× the stem width, and the lamina on each side has a small to large lacinia near the lobe base (the lamina otherwise has 1–2 accessory processes). Trigones are minute. I have observed gynoecia only in early bract fusion stages; Stephani stated that perianths are juvenile but describes them as more mature than those I have seen.

11) *Lophocolea geheebii* Steph. The protologue states that the type is at G. A Bäuerlen specimen at G that bears label information matching the protologue consists of sterile shoots together with those bearing androecia. That collection also has one shoot bearing a gynoecium; it is in the pre–leaf fusion stage and is included within the bracts. The gynoecium is contrary to the protologue, which states that perianths are oblong, and to the illustration in the Stephani icones (*Lophocolea* no. 107b), which clearly shows fused perianth lobes. However, the young gynoecium matches the protologue and icones in having perianth lobes that have large teeth and that are "longe bifidis," and also in bract and bracteole characters. A few other deviations from the protologue may be noted. Trigones are small and concave sided, and not "majusculis" as stated in the protologue, and the underleaves are narrowly connate on 1 side, not free. The above deviations aside, the Bäuerlen collection agrees with the protologue, and I consider that collection to constitute original material. Stephani perhaps dissected the only mature perianth, illustrated the mouth (lobes spread and flattened), and discarded that dissection. I have been unsuccessful in attempts to locate at various herbaria a duplicate of the Bäuerlen specimen (BM, BR, E, FH, GOET, H, HBG, L, M, MANCH, MEL, PC, S, and W; all = *absens*). The specimen represents a rather well-developed phase of *C. semiteres*.

12) *Lophocolea forsythiana* Steph. The specimen consists of shoots with young gynoecia (perianths are included within bracts), others with androecia (abundant) and still others that are sterile. Leaves have apices broadly rounded to truncate. Leaf cell trigones are small to medium to (sporadically) large and feebly bulging, depending on the shoot and leaf. The underleaf lamina on each side has a dentiform to laciniiform process. Plants of *Fissidens* are admixed.

13) *Lophocolea fernandeziensis* Steph. The specimen consists of small (ca. 1.6 mm wide), mostly androecium-bearing shoots. Underleaves on sterile shoots are divided nearly to the base, and the lamina on each side has a distinct lacinia. Trigones are small and concave sided.

14) *Lophocolea heterophylloides* var. *crassiflora* Pearson. The underleaf lamina has on each side a laciniiform to lobuliform process and 1–2 accessory teeth or laciniae. Trigones are small to medium and not absent as indicated in the protologue. The perianth-bearing shoot (in micropacket) is rather flaccid, accounting for the rather contorted perianth illustrated by Pearson. The perianth is actually triquetrous, with each lobe bifid.

15) *Lophocolea heterophylloides* var. *decurrens* Pearson. The specimen consists primarily of shoots with young gynoecia with (often repeated) subfloral innovations. The rather shallowly divided underleaves (to 0.6–0.7) have on each side of the lamina a small to large lacinia. Trigones are minute or absent.

16) *Lophocolea calbucensis* Herzog. Leaf apices are often retuse to retuse-1-dentate to short bifid. The underleaf lamina on each side has a laciniiform to lobuliform process and often an accessory tooth. Underleaves are weakly connate on 1 side (the protologue notes that they also may be free). The specimen represents a suboptimal phase of *C. semiteres*.

17) *Lophocolea magnistipula* S. W. Arnell. Two collection numbers (*513*, *1101*) are cited in the protologue; I have seen only material of the latter number. The specimens consist of flaccid plants with a plastic underleaf shape. The underleaf lamina on each side has a laciniiform to lobuliform process and 1–3 accessory teeth and laciniae. Trigones are small.

18) *Lophocolea squamata* Herzog. The specimen represents a rather large phase of *C. semiteres*. The underleaf has on each side a laciniiform to lobuliform process and small trigones. Leaf apices are broadly rounded to feebly retuse to sporadically retuse. Androecia are common.

The holotype is in the personal herbarium of A. D. Banwell (introductory note in Herzog, 1949).

DISTRIBUTION—The variety is pan-south temperate and variable in frequency in different parts of its range (Engel, 1992a), occurring in Australasia, southern South America, Juan Fernandez, Falkland Is., Tristan da Cunha, Inaccessible Is., and South Africa. In Australasia it occurs in New Zealand (Stewart Is.; South Is., sea level–1650 m; North Is., sea level–550 m), Antipodes Is., Chatham Is., Australia: Tasmania (sea level–1050 m), Victoria (220–1150 m), A.C.T. (600–1900 m), New South Wales (340–1370 m), Queensland, South Australia (200 m), Western Australia (230–650 m). The variety also occurs in the oceanic Isles of Scilly (Paton, 1965), Scotland (Long, 1982), Belgium, and the Netherlands (Stieperaere, 1994); see also Paton (1999).

ECOLOGY—In Western Australia the variety occurs in forests on rotted logs (commonly *Eucalyptus*) and on sandy soil of stream banks. It also occurs on the large, domelike granite outcrops that occur at several sites in Western Australia, including Mt. Chudalup (Chudalup State Forest) and Devils Slide (Porongurup Range; see Smith, 1962), and here the variety occurs in protected niches such as on soil over shaded, moist rock surfaces. (See also comments under *C. canaliculatus*, p. 106.)

In New Zealand, the variety occurs in a number of different niches. For example, it occurred on an old, rotting, decorticated, fallen, exposed log in a stream valley under an open canopy of *Beilschmiedia tawa* and *Weinmannia silvicola*, with subcanopy dominants of *Schefflera digitata*, *Cyathea dealbata*, and *C. smithii* and a shrub layer of *Freycinetia baueriana* and *Cortaderia* (Kaimai Range, spur ESE of Ngatamahinerua, 405 m, South Auckland Prov.). At Puketi State Forest (Waihoanga Creek at head of Waihoanga Gorge Kauri Walk, Northland) plants occurred at 180 m as scattered shoots on bark of *Coriaria arborea* overhanging a stream at the margin of an *Agathis australis* forest (*Engel, von Konrat & Braggins 27756* [F]). Also found at ca. 1400 m on the side of a sink hole in a marble karst area on the slopes of Mt. Owen in a region of very steep topography with numerous sink and erosion holes with a mosaic vegetation of scrub, tussockland, grassland, herbfields, and small tarns (Kahurangi Natl. Park, Western Nelson Ecological Prov.). In open, exposed sites, it may be one of the few hepatics present. For example, NE of Kawerau along state highway 30 (project area administered by Norske Skog Tasman and Wildlands Consultants), plants were well-developed and rather common at 20 m in open grass and scrub vegetation with planted *Leptospermum scoparium*, *Pseudopanax crassifolium*, and *Podocarpus totara* (Volcanic Plateau Ecological Prov., North Is.). At this site, plants occurred, e.g., on the floor adjacent to a stump base (*Engel & von Konrat 27984* [F]). *Chiloscyphus semiteres* may occur on exposed tree roots at the edge of the sea in coastal forest remnants dominated by *Metrosideros excelsa* and *Vitex lucens* (*Engel 20278*).

Specimens Seen (selected)—**NEW ZEALAND. CAMPBELL IS.:** Buchanan Valley, 150 m, *Meurk H8297* (WELT). **STEWART IS.:** Ringaringa Bay, *L. M. C. s.n.* (CHR). **SOLANDER IS.:** SE pen., 100–140 m, *Johnson s.n.* (CHR); SW ridge, 190 m, *Johnson s.n.* as *L. novaezeelandiae* (CHR); N side plateau, 270 m, *Johnson s.n.* as *L. novaezeelandiae* (CHR). **SOUTH ISLAND. SOUTHLAND:** Bluff Hill, ca. 60 m, *Allison H 5166* (CHR); 2 mi. from Awarua Bay, near Bluff, *Martin s.n.* (CHR); Awarua bog, near Bluff, *Martin s.n.* (CHR); Fiordland Natl. Park, along flat of Spey River, near W arm of Lake Manapouri, on Doubtful Sound Track, ca. 190–230 m, *Schuster 52619* (F); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18852* (F). **OTAGO:** Nugget Point, *Simpson s.n.* (CHR); Otago Peninsula, near Otakau, sea level, *Allison H 1351* (CHR); Akatore, 20 mi. SW of Dunedin, ca. 5 m, *Child H 985* (F); Akatore Stream, S of Dunedin, *Allison H 1358* (CHR); near Berwick, S of Dunedin, ca. 45 m, *Allison H 1372* (CHR); near Outram, S of Dunedin, ca. 60 m, *Allison H 1383* (CHR); Dunedin Botanic Gardens, ca. 30 m, *Child H 611* (F); Dunedin, St. Kilda Golf Course, sea level, *Child H 78* (F); ibid., Cosy Dell, ca. 150–245 m, *Child H 1643* as *L. dalliana*, *H 1650*–c. ♂, *H 2427*–c. ♂ (F); Lee Stream, ca. 305 m, *Child H 2514* (F); Mt. Cargill, W side, N of Dunedin, ca. 455 m, *Child H 765* (F); Beaumont, ca. 150 m, *Child H 3420* as *L. novaezeelandiae* (F); Hindon, ca. 305 m, *Child H 910* (F); Rocklands, Old Dunstan Road, ca. 455 m, *Child H 1088* (F); Rock and Pillar, ca. 760 m, *Child H 3024* (F); Paradise, Jordan River, head of Lake Wakatipu, ca. 365–455 m, *Child H 2419* (F); ibid., Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, *Child H 1244*–c. ♂ (F); Chinamans Bluff Flat, Dart Valley, N of N end of Lake Wakatipu, ca. 550 m, *Child H 1291* as *L. novaezeelandiae* (F); Lindis Pass, 1 mi. S of pass, ca. 1220 m, *Child H 220* (F); Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, 1370–1470 m, *Engel 17900A* (F). **WESTLAND:** Kelly Creek, ca. 150 m, *Child H 345* (F). **CANTERBURY:** Hunter Hills, Bluecliffs Station, ca. 215 m, *Macmillan 76/274* (CHR); Rakaia River, Great Is., *Macmillan 70/160* (CHR); Banks Peninsula, Akaroa Heads, Dan Rogers Creek, ca. 305 m, *Macmillan 75/150* (F); ibid., Kaituna Valley, *Hatcher 1209* (F); ibid., Packhorse Track, SW of Mt. Herbert, ca. 150 m, *Macmillan 77/275* (CHR); Sebastopol, Mt. Cook region, ca. 1160 m, *Wilson 2522* (CHR); Christchurch, Riccarton Bush, *Macmillan 76/418* (CHR); Christchurch Garden, *Macmillan s.n.* (CHR); E of Darfield, ca. 185 m, *Macmillan 72/965* (CHR); Waimakariri River, E of Burnt Hill, ca. 230 m, *Macmillan 71/458* (CHR); Lake Ellesmere, S of Christchurch, sea level, *Child H 332* (F); Waiau River, ca. 245 m, *Macmillan 75/124* (CHR). **NELSON:** Kahurangi Natl. Park, flank of Mt Owen, ca. 1400 m, *Engel & Matt von Konrat 28607* (F); Nelson Lakes Natl. Park, Second Basin, *Simpson 3920* as *L. heterophylloides* (CHR); St. Arnaud Range, Rainbow Ski Field, ca. 1650 m, *Brown 87/18* (AK); Cape Foulwind, ca. 30 m, *Child H 3598* (F); Nelson City, Tehunanui, *Allison H 6466* (CHR); Karamea Beach, ca. 5 m, *Child H 3508* (F); Farewell Spit, sea level, *Patterson s.n.* (AK). **MARLBOROUGH:** Blenheim, Wither Hills, *Healy s.n.* (CHR); Pelorus Bridge, *Braggins s.n.* (AK); Cook Strait, Outer Trio Is., *Macmillan 71/556* (CHR); ibid., Stephens Is., *Macmillan 71/179* (CHR); ibid., Little Brother, *Collett s.n.* (CHR). **NORTH ISLAND. WELLINGTON:** Cape Turakirae, *Braggins s.n.* (AK); Princess Bay, *Braggins s.n.* (AK); Wellington, Hawkins Hill, *Moss s.n.* (AK); ibid., Eastbourne, Kowhai Street track, *Moss s.n.* (AK); Wiltons Bush, *Mason s.n.* as *L. pallida* (CHR); Wairarapa, near Martinborough, *Mues NZ 18a* (F); Lake Wairarapa, Western Lake Reserve, *Braggins H 147* (AK); Keith George Memorial Park, near Silverstream, Upper Hutt, *Mues NZ 18* (F); Elsden Reserve, Porirua, *Braggins s.n.*–c. ♂ (AK); suburb of Masterton, Upper Plain, Wairarapa, *Allison H 7168* (CHR); Mt. Bruce, Masterton, *Kemble Welch 44* (CHR); E Wairarapa, New Range Road, Big Hill, *Braggins H 95* (AK); Mt. Marima, ca. 185 m, *Zotov s.n.* as *L. heterophylloides* (CHR); Mt. Arawaru, *Zotov s.n.* as *L. heterophylloides* (CHR); near Fitzherbert, *Zotov s.n.* as *L. pallida* (CHR); ibid., Palmerston N, *Zotov s.n.* as *L. heterophylloides* (CHR); Palmerston N, *Zotov s.n.* as *L. heterophylloides* (CHR); near Marton, *Zotov s.n.* as *L. heterophylloides* (CHR); Wanganui, *Allison H 3395* (CHR). **HAWKE'S BAY:** Wairoa, "Kiwi," *Hodgson s.n.* as *L. heterophylloides* (AK), *34*, *373*, *374* (CHR); ibid., Hurumua, *Hodgson 617* (CHR); near Wairoa, *Hatcher 1270* (F); Morere, *Hatcher 28*–c. ♂ (F). **GISBORNE:** Lake Waikaremoana, Ariwaniwa Falls, *Jeffries s.n.* as *L. dalliana* (CHR). **SOUTH AUCKLAND:** Tokaanu, thermal area, *Braggins s.n.* (AK); Kaingaroa Plains, "Mile Plantation," *Allison H 3395* (CHR); E of Waiotapu Valley, S of Rotorua, ca. 550 m, *Allison H 3696* (CHR); Waiotapu, N of Reporoa, *Child H 21* (F); near Waikato River, above Atiamuri, S of Rotorua, *Allison H 73* (CHR); near Atiamuri, S of Rotorua, *Allison H 3701* (CHR); Rainbow Mtn., S of Rotorua, *Allison H 3364* (CHR);Waimangu Thermal Valley, *Braggins s.n.*–c. per. (AK); ibid., S Crater, *Braggins s.n.*–c. per. (AK); ibid., Warbrick Terrace area, *Braggins s.n.*–c. per., *s.n.*–c. ♂ (AK); ibid., SW of Lake Rotomahana, *Schuster 67-3750* (F); Arikikapakapa Reserve, Rotorua, *Allison H 3428* (CHR); Te Kauri Park, Kawhia, *Parkinson s.n.* (AK); near margin of Lake Rotoehu, *Allison H 3401* (CHR); between Lake Rotoehu and the Bay of Plenty, *Allison H 3402* (CHR); Pongakawa River, Bay of Plenty, *Allison H 3407* (CHR); Whatipu, *Lynch s.n.* (AK); Kaimai Mamaku Forest Park, Kaimai Range, spur ESE of Ngatamahinerua, headwaters of Poupou Stream, ca. 2 km W of North–South Track, 405 m, *Engel & von Konrat 23590* (F); Coromandel Peninsula, near Coromandel, *Rawson R 12*–c. ♂ (CHR); Mercury Group, Middle Is., ca. 60 m, *Cameron 2506* (AK). **NORTH AUCKLAND:** Anawhata, *Braggins s.n.*–c. ♂ (AK); Remuera, 50 m, *Scofield s.n.* (AK); Swanson, *Braggins s.n.* (AK); Waitakere, ca. 120 m, *Child H 2238* (F); West Tamaki Head, *Kirk s.n.* as *L. minor* (CHR); ibid., track to Karaka Bay, *Braggins s.n.* as *L. heterophylloides* (AK); Auckland, Government House, *Macmillan 76/318* (AK); ibid., University of Auckland grounds, *Braggins s.n.*–c. ♂ (AK); ibid., Kepa Road Reserve, *Idoine s.n.* (AK); Waitamata Harbour, Rangitoto Is., 10–35 m, *Braggins s.n.*–c. ♂ (AK); same loc., *Moore s.n.* as *L. pallida* (AK); Woodhill, *Robbins (1)* as *L. heterophylloides* (AK, CHR); Woodhill Forest, ca. 10 m, *Braggins 87/64* (AK); Mangawai Heads, 2 km N along ocean beach from road end, sea level, *Braggins s.n.* (AK); Hen and Chickens Group, Lady Alice Is., ca. 100 m, *Beever 8-10a* (AK); ibid., Whatupuke Is., ca. 25–60 m, *Beever 8-48a* (AK); Kawerua, *Haywood s.n.*–c. ♂ (AK); track to Ti Point Scenic Reserve, N head of Whangateau Harbour, S of Leigh, sea level, *Engel 20278*–c. ♂ (F); Waipoua Forest, Te Matua Ngahere, Big Tree, *Taylor s.n.* (AK); ibid., *Allison H 746* (CHR); Omapere, Hokianga, ca. 15 m, *Child H 2182*–c. ♂ (F); Poor Knights Group, Aorangi Is., SE coast, ca. 5 m, *Beever s.n.* (AK); ibid., ibid., NE slope Oneho Hill, ca. 200 m, *Beever s.n.* (AK); near Taipa, *Taylor 73/231* (AK); Onepu Crownland, N of Houhora, *Segedin s.n.* (AK). **LITTLE BARRIER IS.:** *Braggins 84/132b* (AK); Te Titoki Point, *Braggins 80/975a* (AK); E Cape Hut, *Braggins 80/322*–c. ♂ (AK); ibid., *Braggins et al. 80/334* as *Clasmatocolea* sp. (AK). **GREAT BARRIER IS.:** *Kirk 148* (CHR). **ANTIPODES IS.:** ca. 15 m, *Godley s.n.* (CHR). **CHATHAM IS.:** Nikau Bush Scenic Reserve, ca. 60 m, *de Lange CH1041* (AK, F). **TASMANIA.** S Bruny Is., Adventure Bay, Adventure Beach, sea level, *Engel 16667* (F); Port Cygnet, Agnes Rivulet, *Weymouth 232* as *L. heterophylloides*–c. ♂ (HO); 0.5 mi. N of Cygnet on road to Kingston, *Norris 26671* (F); Huon, Gardner's Bay, *Weymouth 237b* as *L. heterophylloides* (HO); ibid., road from Gardner's Bay to Peppermint Bay, *Weymouth 237* as *L. heterophylloides* (HO, M, STR); Tasman Peninsula, Isle of the Dead, Port Arthur, *Weymouth 633* as *L. fissistipula*, *634* as *L. heterophylloides* (HO); ibid., Wedge Bay, *Rodway s.n.* as *L. canaliculata* (HO); ibid., Waterfall Bay, sea level–150 m, *Norris 27704* (F); ibid., ibid., Camp Falls, 150–240 m, *Engel 12701*–c. per. (F); ibid., along Block and Stable Creek, at Lake Leake Road, ca. 400 m, *Norris 30669* (F); Mona Vale, near Ross, *Weymouth 860* as *L. heterophylloides* (HO); W facing slope of Mt. Arthur, Pipers River, NE of Launceston, ESE of Lilydale, 850 m, *Engel 15363*–c. ♂ (F); along S Esk River, about 0.5 mi. N of Fingal, *Norris 28256* (F); St. Mary's, ca. 245 m, *Weymouth 1314* as *L. trialata* (HO, M), *1345* as *L. lauterbachii*, *1353* as *L. oldfieldiana* (HO); St. Patrick's Head, ca. 670 m, *Weymouth s.n.* as *L. macroloba*, *1251* as *L. oldfieldiana* (HO); St. Mary's Pass, The Glen, ca. 275 m, *Weymouth 1256* as *L. subemarginata*, *1325* as *L. longistipula*, *1341* as *L. canaliculata* (HO); along Scottsdale to St. Helens Highway, about 0.5 mi. E of Parr Rivulet, ca. 300 m, *Norris 31886* (F); ibid., about 1 mi. E of bridge at Great Forester River, *Norris 31861* (F); Ringarooma, Ruby Flat forest, ca. 275 m, *Weymouth 1576* as *L. heterophylloides* (HO); S slope of Mt. Cameron, 300–350 m, *Norris 28444* (F); about 2 mi. E of Longford, ca. 150 m, *Norris 27171* (F); Launceston, Cataract Gorge, *Rodway s.n.* as *L. forsythiana* (HO); ibid., ibid., *Weymouth 1295* as *L. oldfieldiana*, *1302* as *L. macrostipula* (HO); ibid., ibid., Giant's Cave, *Weymouth 1297* as *L. geheebii* (HO); ibid., S Esk River, Trevallyn Gully, *Weymouth 43* as *L. heterophylloides* (HO, M); Lilydale Falls, 2.6 km by road N of Lilydale, NNE of Launceston, ca. 200 m, *Engel 15200*–c. per. (F); near Coal Bluff, sea level–50 m, *Norris 30233* (F); near Catamaran, *Weymouth 1523* as *L. canaliculata* (HO); Recherche, near Leprena, *Weymouth 1527* as *L. heterophylloides* (HO); Hastings, Shingle Hill,, ca. 75 m, *Weymouth s.n.* as *L. fissistipula* (HO); along Dover to Raminea Road, about 1 mi. N of Raminea, near sea level, *Norris 27153*–c. ♂ (F); Arve Valley, Arve Loop Road, near junction with Arve Road, N of Hartz Mtn. Natl. Park, 150–200 m, *Engel 12868* (F);Tahune Forest Reserve, near Huon River, N of Hartz Mtn. Natl. Park, 70 m, *Engel 19883*–c. sporo. + ♂ (F); ibid., off Pine Track, along Huon River, N of Hartz Mtn. Natl. Park, 70 m, *Engel 19924*–c. ♂ (F); along Huon River, about 0.5 mi. N of end of Scotts Peak Road, ca. 300 m, *Norris 30828* (F); Huon River, Southbridge, *Weymouth 665* as *L. heterophylloides* (HO); Kermandie River, near Huonville, 140 m, *Ratkowsky 77/164* (HO); Tysons Track, near Mountain River settlement, 500 m, *Ratkowsky 77/170* (HO); Sandfly, *Rodway s.n.* as *L. gunniana*–c. sporo., *s.n.* as *L. variabilis*–c. sporo. (HO); Pipeline Track, Neika, 500 m, *Ratkowsky 77/167*–c. ♂ (HO); gully near Fern Tree, *Rodway s.n.* as *L. heterophylloides*–c. sporo. + ♂ (HO); along trail from Fern Tree to Silver Falls, ca. 500 m, *Norris 29179* (F); Mt. Wellington, ca. 305–610 m, *Rodway s.n.* as *L. heterophylloides*–c. sporo., *s.n.* as *L. macrostipula*–c. sporo., *s.n.* as *L. forsythiana* (HO); ibid., Tysons Trail, Mountain River, *Ratkowsky H 1418* (HO); ibid., St. Crispins Track, *Weymouth 97* as *L. heterophylloides* (HO); ibid., Watchorn's Creek, *Weymouth 495* as *L. heterophylloides* (HO); ibid., Deep Creek, *Weymouth 301* as *L. heterophylloides* (HO); ibid., ibid., *O. Weymouth 530* as *L. subemarginata* (HO); ibid., near The Springs, *Ratkowsky 78/152* (HO); ibid., ibid., ca. 760 m, *Weymouth 1556* as *L. forsythiana* (F, HO); ibid., The Springs Track, *Weymouth 274* as *L. fissistipula* (HO); ibid., Guy Fawkes Rivulet, *Weymouth 1211* as *L. multipenna*–c. ♂ (F, HO); ibid., McRobie's Gully, *Weymouth s.n.* as *L. heterophylloides* (HO); ibid., Fern Glade Track, ca. 460–520 m, *Engel 13052*–c. ♂ + per. (F); Myrtle Forest, SW of Collinsvale, ca. 2.3 km N of Collins Bonnet, 680 m, *Engel 12662*–c. per. (F); Kingston Beaeh Track, sea level, *Ratkowsky 78/150* (HO); Mt. Nelson, *Rodway s.n.* as *L. oldfieldiana* (HO); Sandy Bay Rivulet, Hobart waterworks, ca. 150 m, *Weymouth 480* as *L. heterophylloides* (HO); Knocklofty, near Hobart, ca. 245 m, *Weymouth s.n.* as *L. forsythiana* (HO); ibid., Sugar Loaf Flat, near Hobart, *Weymouth 954* as *L. oldfieldiana* (HO); Huon Road, near Hobart, ca. 305 m, *Weymouth 871* as *L. heterophylloides* (HO); Hobart, Cascades, *Rodway s.n.* as *L. forsythiana* (HO); New Town Rivulet, near Hobart, *Weymouth 723*, *726* both as *L. heterophylloides* (HO); Proctor's Road, *Rodway s.n.* as *L. heterophylloides*–c. sporo. (HO); Mt. Dromedary, Dean Brook, *Weymouth 844* as *L. heterophylloides* (HO); Uxbridge, *Rodway s.n.* as *L. heterophylloides* (HO); Mt. Field Natl. Park, Russell Falls, *Rodway s.n.* as *L. gunniana* (HO); Junee River, *Rodway s.n.* as *L. spongiosa*–c. sporo. (HO); track to Lake Judd, S of Mt. Eliza, E of Lake Pedder, 520 m, *Engel 13749* (F); Adamsfield Track, between Florentine River and junction with Tim Shea Track, W of Mt. Tim Shea, E of Lake Gordon, 400 m, *Engel 13612* (F); Macquarie Harbour, Birch's Inlet, *Rodway s.n.* as *L. macrostipula* (HO); Lyell Highway, near Liapootah Dam Turnoff, S of Tarraleah, 520 m, *Engel 12964*–c. per. + ♂ (F); off Lyell Highway, near turnoff to Tarraleah, *Engel 12989*–c. ♂ (F); 5 mi. NE of Tarraleah, *Norris 33271* (F); Cradle Mtn.–Lake St. Clair Natl. Park, track to Echo Point hut, 700 m, *Ratkowsky 78/149* (HO); along Lyell Highway, about 1 mi. W of Clarence River, *Norris 33371* (F); along Franklin River, at Frenchman's Cap Trail crossing, ca. 400 m, *Norris 31205*–c. per. (F); Macquarie Harbour, Kelly's Basin, sea level, *Moore s.n.* as *L. heterophylloides* (HO); Zeehan, western mine, ca. 200 m, *Weymouth 1461* as *L. heterophylloides* (HO); NE Dundas Tramway (abandoned), W of Williamsford, SW of Rosebery, ca. 400 m, *Engel 16516*–c. ♂ (F); near Williamsford, ca. 400 m, *Norris 31568* (F); Mackintosh River, at Murchison Highway, *Norris 33776* (F); Mt. Bischoff, *Rodway s.n.* as *L. rupicola* (HO); Great Lake, *Rodway s.n.* as *L. forsythiana* (HO); Cradle Mtn.–Lake St. Clair Natl. Park, Cradle Mtns., *Rodway s.n.* as *L. bridelii* (HO); ibid., near SW end of Lake Dove, on track from Ballroom Forest to Lake Wilks, 1050 m, *Engel 14032* (F); ibid., NE side of Crater Lake, 1040 m, *Engel 14075* (F); ibid., along trail from Lake Dove to Lake Rodway, *Norris 34129* (F); ibid., above Pencil Pine Creek, off track between Quailes Hill and Pencil Pine Lodge, E of Pencil Pine Lodge, 770–800 m, *Engel 19617* (F); Lake Lea, ca. 800 m, *Norris 27381* (F); ridge SE of Black Bluff, near junction of access road to plateau area and road to Devonport gold mines, N facing slope, S of Burnie, 1000 m, *Engel 16241*–c. ♂ (F); W Downs, terminus of Basils Road, SSW of Burnie, 575 m, *Engel 16033*–c. ♂ (F); rivulets near Cheshunt, near Deloraine, *Archer et al. s.n.* as *L. heterophylloides*–c. sporo. (HO); Notley Fern Gorge, SE of Glengarry, NW of Launceston, 180–210 m, *Engel 15358*–c. ♂ (F); Asbestos Range Natl. Park, Badger Head, on Bass Strait, ca. 30 m, *Engel 20164*–c. ♂ (F); vicinity of Croesus Cave, near bridge over Mersey River, ca. 2.9 km S of Liena, 325 m, *Engel 15937*–c sporo. (F); Wilmot, *Weindorfer s.n.* as *L. macrostipula* (M); above Lake Barrington, near Forth Falls, ca. 150 m, *Norris 27239* (F); near Devil's Gate Dam, ca. 150 m, *Norris 27222* (F); River Leven, about 1 mi. S of Leven Hill, ca. 200 m, *Norris 32505* (F); Mt. Montgomery, *Norris 33913*, *33950* (F); Ferndene, *Norris 33959* (F); Fern Glade, Emu River, SE of Burnie, sea level, *Engel 15611* (F); Detention Falls, SSW of SistersCreek, W of Wynyard, 190 m, *Engel 19665* (F); Rocky Cape Natl. Park, vicinity of Rocky Cape, N coast between Smithton and Wynyard, ca. 120 m, *Engel 16056* (F); Circular Head, S Road Forest, *Weymouth 1198* as *L. heterophylloides* (HO); Trowutta, *Rodway s.n.* as *L. geheebii*–c. sporo. (HO). **AUSTRALIA. VICTORIA:** Mt. Donna Buang, 4.5 km NNW of Warburton, 1150 m, *Streimann 36253*–c. sporo. (NY); near McMahons Creek, 10 km NE of Warburton, 220 m, *Streimann 978* (CBG); Bonang River, ca. 6 km from Bonang toward Orbost, 700 m, *Verdon 1116*–c. ♂ (CBG); Hughes Creek, 14 km E of Seymour, on Tarcombe Road, 550 m, *Streimann 15538* (CBG); Berringama, 22 km W of Corryong, 400 m, *Butler 51*–c. ♂ (CBG); Myers Creek, 8 km N of Healesville, 350 m, *Streimann 1004*–c. sporo. (CBG). **A.C.T.:** Clear Range, Mt. Clear, 64 km S of Canberra, 1590 m, *Streimann 10616* (CBG); Bimberi Range, Mt. Bimberi, 49 km SW of Canberra, 1900 m, *Streimann 9728* (CBG); Booroomba Rocks, 30 km SSE of Canberra, 1240 m, *Streimann 9065*–c. ♂ (CBG); Canberra Botanic Gardens, *Beeton B 13* (CBG); ibid., *sin. coll.* (H 172, H 174) (NSW); Brindabella Range, head of Gingera Creek, 43 km SW of Canberra, 1680 m, *Streimann 4198*–c. ♂ (CBG); ibid., Mt. Aggie, 38 km SW of Canberra, 1500 m, *Streimann 7703* (CBG); Tidbinbilla Range, ca. 1220 m, *Adams 1401* (NSW); Tidbinbilla Nature Reserve, 25 km SW of Canberra, 1000 m, *Streimann 1067*–c. sporo. (CBG); Molonglo Gorge, 15 km E of Canberra, 700 m, *Streimann 1826*–c. per. + ♂ (CBG); Canberra–Brindabella Road, 24 km W of Canberra, 850 m, *Streimann 83*–c. sporo. + ♂ (CBG); Black Mtn., 5 km NW of Canberra, 780 m, *Streimann 10339* (CBG); ibid., North Gully, 600 m, *Beeton B 96* (CBG); Uriarra Forest, 20 km WNW of Canberra, 650 m, *Streimann 169*–c. ♂ (CBG); Blue Range Road, head of Uriarra Creek, 1000 m, *Streimann 10209* (F, NY). **NEW SOUTH WALES:** Newington, *sin. coll.* (H 197) (NSW); Great Dividing Range, Big Badja Mtn., 47 km NE of Cooma, 1340 m, *Streimann 5579* (CBG); The Long Plain, 41 km NNW of Adaminaby, 1370 m, *Streimann 1701* (CBG); Nowra, *Watts 866* as *L. heterophylloides* (NSW); Merricumbene Fire Trail, 16 km W of Araluen, 440 m, *Streimann 7318* as *L. pallida* (CBG); Kangarooby State Forest, 16 km S of Gooloogong, 450 m, *Streimann 10389* (CBG); Tinderry Pic, 12 km E of Michelago, 900 m, *Streimann 5184* (CBG); Bago State Forest, 8 km SW of Batlow, 800 m, *Streimann 7408* (CBG); 1 km S of Batlow on Tumbarumba Road, 600 m, *Streimann 1808*–c. sporo. (CBG); Endrick River, 3 mi. E of Nerriga, ca. 610 m, *Adams 1447* (NSW); near Tomerong, *Watts 621* as *L. bridelii*–c. sporo. (FI); Bundanoon, S highland, ca. 660–670 m, *Tindale H 20* as *L. heterophylloides* (NSW, S); Macquarie Pass, 28 km SW of Wollongong, 520 m, *Streimann 4821* (CBG); Stanwell Park, Hopkin's Creek, *Watts s.n.* as *L. heterophylloides*–c. ♂ (M); surroundings of Sydney, niece of *Kayser s.n.* as *L. heterophylloides*–c. sporo. (M); between Homebush and Parramatta, *sin. coll.* (H 198) (NSW); Broula Range, 27 km ENE of Grenfell, 580 m, *Streimann 10378* (CBG); Lane Cove River, Kitty's Creek, *Watts 1098* as *L. wattsiana* (NSW); Emu Plains, *Watts 190* as *L. bridelii*–c. ♂, *206* as *L. bridelii* (FI); Blue Mtns., Mt. Tomah, ca. 960–975 m, *Tindale et al. H 2* as *L. heterophylloides*–c. sporo. + ♂ (NSW, S); ibid., track to Wentworth Falls, *Braggins s.n.* (AK); Somersby Falls, near Gosford, *Braggins s.n.* (AK); Mt. Canobolas, Federal Falls, 10 km SW of Orange, *Streimann 9205* (CBG); Hamilton, near Newcastle, *Watts 203* as *L. bridelii*–c. ♂ (FI, NSW); Minmi, near Newcastle, *Watts 315* as *L. heterophylloides* (NSW); Gloucester Tops, 42 km WSW of Gloucester, 1280 m, *Streimann 1533* (CBG); Gloucester River, 35 km WSW of Gloucester, 400 m, *Streimann 1596* (CBG); escarpment below Waihou Trig. Station, 25 km NW of Coffs Harbour, 340 m, *Streimann 6560* (CBG); Wardell, *sin. coll.* (H 201)–c. ♂ (NSW); Richmond River, lagoon, 7 mi. beach, *Watts 51* as *L. heterophylloides* (NSW); Cubbing, Alstonville Road, 5 ⅙ mi. from Ballina, *Watts 285* as *L. heterophylloides*–c. sporo. + ♂ (NSW); ibid., *Watts H 206* (NSW). **QUEENSLAND:** Near Brisbane, *Simmons s.n.* as *L. bridelii* (FI). **SOUTH AUSTRALIA:** 10 km SSE of Western River, N coast of Kangaroo Is., *Seppelt 0787* (HO); Mt. Lofty Range, 3 km SE of Williamstown, 200 m, *Streimann 4124* (CBG). **WESTERN AUSTRALIA:** King Georges Sound, *Webb s.n.* as *L. heterophylloides* (BM); Walpole-Nornalup Natl. Park, near intersection of Hilltop and Gully Roads, E of Walpole, *Engel 13429A* (F); Chudalup State Forest, Mt. Chudalup, NE of Point d'Entrecastreaux, along Wheatley Coast Road, 230 m, *Engel 13402* (F); Porongurup Natl. Park, Devils Slide, 440–650 m, *Engel 13467* (F); ibid., between and including Morgans View and Nancys Peak, 640 m, *Engel 13509* (F); ibid., Scenic Drive, near Outlook Rock, *Engel 13515* (F); The Cascades, Lefroy Brook, S of Pemberton, *Engel 13408*–c. ♂ (F); Pemberton, *Thiers 43211* (F); ibid., *G. G. Smith 78* as *L. squamata* (UWA); ibid., Karriwald, *Walter 16* as *L. heterophylloides* (M); Beedelup State Park, ca. 11 km W of Pemberton, *Engel 13391*–c. per. (F); ibid., ibid., Beedelup Falls, *Engel 13396*–c. per. + ♂ (F); Mammoth Cave (limestone), N of Augusta and W of Forest Grove, *Engel 13374*–c. ♂, *13375* (F); Swan River, *Drummond s.n.* as *L. heterophylloides* (M), *s.n.*as *J. recubans*, nom. herb. (BM); ibid., *Campbell s.n.* as *L. heterophylloides* (BM).

***Chiloscyphus semiteres* var. *retusus* J. J. Engel, var. nov.**

A varietate typica apicibus saepe retusis vel curto-bifidis, lobis pleurumque rotundatis differt.

HOLOTYPE—Australia, New South Wales, Murrumbidgee River, Rules Point, 37 km NW of Adaminaby, *Streimann 7482* (CBG!)

Leaf apices variable: undivided to retuse-short bifid, the lobes normally rounded, the leaf apex occasionally with 1 of lobes acute but never with a pair of acute lobes; trigones small and concave sided to medium and straight sided; underleaf ca. 2–4× stem width, the disc on each side with a prominent laciniiform to lobuliform process and often an accessory tooth.

DIFFERENTIATION—Variety *retusus* is distinctive in having most shoots with at least some leaves retuse-short bilobed. The variety should not be confused with suboptimal var. *semiteres*, which may have several to many leaves with retuse-bidentate apices. Plants of var. *retusus* are vigorous, and have well developed underleaves ca. 2–4× the stem width.

DISTRIBUTION AND ECOLOGY—Known only from Australia (A.C.T., 1350 m; New South Wales, 700–1390 m), where it occurs on moist, shaded rock in open stunted or tall *Eucalyptus* forests. In such situations, it sometimes occurs in *Leptospermum* and *Casuarina*-fringed watercourses. It also may be found in short grasslands on shaded rock faces. (See also comments under species, p. 97)

SPECIMENS SEEN—**AUSTRALIA. A.C.T.:** Bimberi Range, Mt. Bimberi, 49 km SW of Canberra, *Streimann 4379* (CBG); Smokers Flat, 1350 m, *Streimann 4434* (CBG). **NEW SOUTH WALES:** Mt. Canobolas, 8 km SW of Orange, 1390 m, *Streimann 9149* (CBG); Hyland State Forest, head of Hyland Creek, 22 km NW of Dorrigo, 1040 m, *Streimann 6773* (CBG); Tumut 1 Power Station, 2 km SW of Cabramurra, 700 m, *Streimann 1711* (CBG).

Chiloscyphus canaliculatus Gottsche, Lindenb. & Nees

Chiloscyphus canaliculatus Gottsche, Lindenb. & Nees, Syn. Hep. 710. 1847. *Jungermannia canaliculata* Hook. f. & Taylor, London J. Bot. 3: 563. 1844, *non J. canaliculata* Nees, Hep. Javanicae 10. 1830. *Lophocolea heterophylloides* var. *canaliculata* (Gottsche, Lindenb. & Nees) Carrington & Pearson, Pap. & Proc. Roy. Soc. Tasmania 1887: 51. 1888. *Lophocolea canaliculata* (Gottsche, Lindenb. & Nees) Steph., Bull. Herb. Boissier 6(9): 786. 1906 (= Spec. Hep. 3: 86). *Chiloscyphus semiteres* var. *canaliculatus* (Gottsche, Lindenb. & Nees) J. J. Engel, Contr. Univ. Mich. Herb. 18: 109. 1992. Lectotype (*fide* Engel, 1992a): New Zealand, "Falls of Waitangi," *Hooker s.n.* (FH!–c. per. + ♂).

Plants soft, loosely prostrate to slightly ascending, pale green to light yellowish green to very pale whitish-green, dull-opaque, with a hazy or milky appearance; shoots usually to 1.2 mm wide. Branches common, of *Frullania* and lateral-intercalary types. Stems rather narrow for plant size, 9–10 cells high, the cortex moderately differentiated, in 1(2) rows of smaller, somewhat thick-walled cells, the exposed wall distinctly thickened; medullary cells slightly firm walled. Rhizoids in an ill-defined zone from stem at base of underleaves. Leaves alternate, dorsally assurgent, the distal and dorsal portions broadly to sharply deflexed, occasionally with all or major portion of leaf subvertical; leaves widely spreading, rather closely imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip. Leaves with a broad adaxial concavity, subsymmetrically oblate; apex undivided and entire, broadly rounded to truncate; margins entire, the dorsal broadly curved, deflexed, at times forming a cnemis, short decurrent, the ventral curved much like the dorsal margin or a little more strongly so, plane. Leaf cells with walls thin, trigones normally large and bulging to knot-like (in shade forms medium and straight sided to weakly bulging), the trigones (4.8)6–7.2(8.4) µm, the ratio of trigone diameter to length of intervening thin wall between trigones variable: 1:(0.9)1.2–2.6(3.2); median leaf cells 24–30 µm wide, 29–34 µm long; surface smooth. Oil-bodies occupying conspicuous portion of cell lumen, greyish orange to chocolate brown at low magnification, light brown at higher magnification, 3–7(9) per cell, coarsely granular to coarsely papillose, the spherules bulging from membrane, the oil-bodies nearly always spherical, often with a depression or crease. Underleaves much smaller than leaves, normally 1–1.5× stem width, narrowly connate on 1 or both sides, insertion sporadically slightly asymmetric, crescent shaped, the underleaves slightly spreading in basal sector, approximate to weakly imbricate, plane to slightly convex (ventral view) or (var. *concavus*) distinctly concave, subrectangular to narrowly ovate; apex 2-lobed to 0.6–0.8 or more, never 4-lobed; lobes ± parallel to moderately diverging, narrowly acute to acuminate, the lobe margins entire; lamina margins mostly entire or dentiform to ciliiform, only sporadically small-laciniiform.

Asexual reproduction absent.

Plants dioecious. Androecia on main shoots, often composed of numerous (up to 18) bract pairs, subfolious, the bracts foliaceous, of similar basic shape as vegetative leaves but slightly smaller, widely spreading, the distal often slightly reflexed, the imbrication much as in leaves, the lobule small in proportion to bract size. Lobule fused toward base with that of opposing bract, the free margin incurved, dilated distally into an incurved, flap-like, tapering, lamelliform process; antheridia 1 per bract, the stalk uniseriate. Bracteoles similar to underleaves. Gynoecia on main shoot or abbreviated lateral-intercalary branches lacking normal vegetative leaves, or on rather long *Frullania*-type branches. Bracts of innermost series larger than leaves, erect and ensheathing perianth at least toward the base, connate dorsally or free from one another but in close proximity, concave in basal portion, ovate to elliptic; apices often undulate, often sharply recurved to revolute, rounded to ± truncate to retuse, with a few broad-based teeth; dorsal

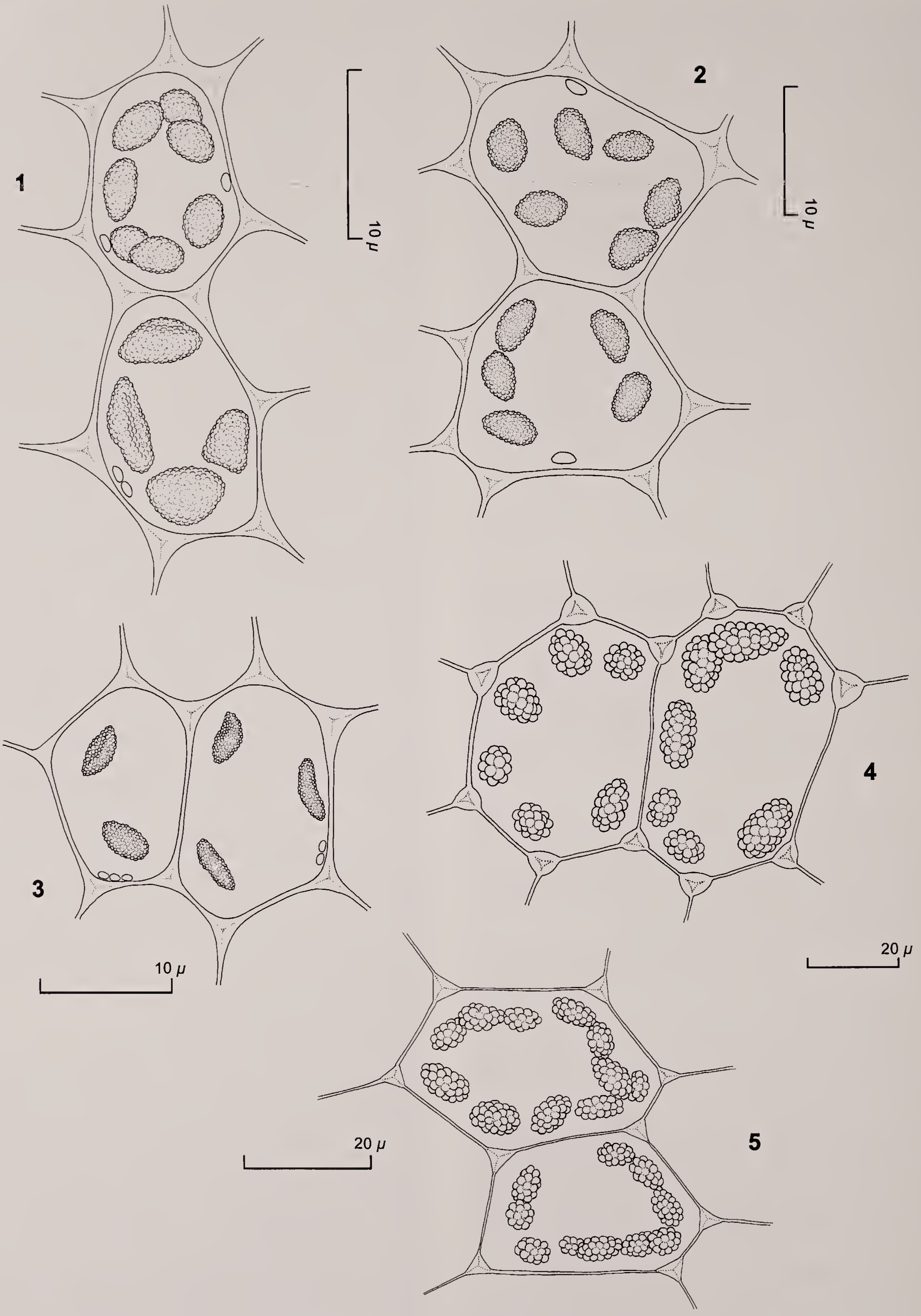

FIG. 37. Oil-bodies. **1.** *Chiloscyphus canaliculatus* Gottsche, Lindenb. & Nees. Median leaf cells, the outline of a few chloroplasts included. **2.** *Chiloscyphus canaliculatus* Gottsche, Lindenb. & Nees. Median leaf cells, the outline of a few chloroplasts included. **3.** *Chiloscyphus spinifer* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. Median lamina cells, the outline of a few chloroplasts included. **4.** *Chiloscyphus trialatus* (Gottsche) J. J. Engel & R. M. Schust. Median lamina cells. **5.** *Chiloscyphus trialatus* (Gottsche) J. J. Engel & R. M. Schust. Median lamina cells. (**1,** from *Engel & von Konrat 28156*, New Zealand, North Is., Southern North Is. Ecological Prov., Mokai Patea Range, W of Ruahine Range and NW of Rongotea Peak; **2,** from *Engel & von Konrat 27444*, South Is., Fiordland, Fiordland Natl. Park, Smithy Creek; **3,** from *Engel & von Konrat 28452*, New Zealand, South Is., Canterbury Ecological Prov., Arthur's Pass National Park, McGrath Creek; **4,** from *Engel 20587*, New Zealand, North

margin often reflexed, entire or with 1–2 broad-based teeth, the ventral margin often undulate, typically entire, sporadically with a broad-based tooth. Bracteoles of innermost series moderately smaller than bracts, ca. 0.6 or more the bract area, narrowly to rather broadly connate on both sides, concave (ventral view), obovate; apices bifid to ca. 0.1–0.35 by acute to acuminate lobes; lamina margins on each side with 1–2 broad-based teeth + at times a few accessory smaller teeth. Perianth longly exserted beyond bracts, sharply trigonous throughout, the ventral side sometimes infolded, the perianths narrowly obovate, not expanding toward the wide, 3-lobed mouth; lobes undivided, with a few to several sharp teeth; keels sharp, with keelar wings absent or present and then low, short and entire or with a tooth. Calyptra extending to ca. 0.5× perianth length.

Seta elevating capsule far beyond perianth mouth, seen only in collapsed state. Capsule short elliptic, the wall 43–48 μm thick, of 5 layers, the outer layer of cells equal to thickness of 2.3–3 of interior strata; outer layer of cells short subrectangular, the radial walls with magenta nodular thickenings mostly on longitudinal walls, those on transverse walls sporadic, often smaller, the exposed tangential wall slightly thickened; intermediate and inner layer of cells subequal in thickness, the intermediate layers with vertical thickenings often tangentially extended; innermost layer of cells irregularly short to long rectangular, the walls with semiannular bands red brown, rather common, narrow, at times incomplete, occasionally forked.

Spores 11–12 μm, pale brown, with faint, dense, low but sharply defined, close, papillae and irregular, short, vermiculate markings that sometimes anastomose, spore:elater diameter ratio 1.2–1.3:1. Elaters somewhat tortuous, 9.1–9.6 μm wide, tapered to tips, the spirals 2.4–2.9 μm wide.

DIFFERENTIATION—This species serves as a "connecting link," of sorts, between *C. semiteres* and *C. rupicola*. Like the latter, it has large to knot-like trigones and often a dull, opaque texture. However, the following characters of *C. canaliculatus* argue against any close affinity: 1) the much greater percentage of terminal branching, 2) the complete absence of leaf dentition on either main shoot or branch leaves, and 3) the ecology is nearly always terricolous or saxicolous, isolated exceptions aside (see below and also Table 10).

Plants are a dull opaque compared with translucent in *Chiloscyphus semiteres*. When plants of *C. canaliculatus* are light yellowish green or a very pale whitish-green, the population stands out as clearly distinct in the field.

VARIATION—A few populations are difficult to place because character expression is atypical of the species, and confusion with other taxa is possible. Such populations match optimal materials of the species in having consistently entire leaves lacking any suggestion of dentition and underleaf lateral armature reduced, being tooth-like to ciliiform or lacking. Two features serve as indicators of problem populations, namely 1) trigones are medium and straight sided to feebly bulging, at least on some shoots, and 2) branching is predominantly lateral-intercalary, with terminal branching only sporadic. Several examples illustrate such problem populations: 1) *Engel 15740*, on bryophyte-covered logs in Tasmania (androecial); 2) *Engel 13143*, from a forest floor in Tasmania (mostly gynoecial); and 3) *Engel 18823*, from the top of a huge log in New Zealand (mostly gynoecial). All examples have branching modalities that approach *C. rupicola*, and the ecology of (1) and (3) is typical of that species. However, the medium and straight-sided trigones are characteristic of *C. semiteres*. Therefore, all atypical populations, especially those that do not key smoothly, must be carefully examined, and particular care should be taken in search for shoots devoid of gametangia. Considerable time was devoted to search for sterile shoots in examples (2) and (3). The several sterile shoots isolated in each collection provided an interesting and useful contrast to gynoecial plants. Whereas fertile shoots have mostly intercalary branching, sterile shoots have at least half of the branches terminal. The higher frequency of terminal branching will exclude *C. rupicola*. Furthermore, some sterile shoots have medium to weakly knot-like trigones, whereas other sterile shoots have trigones weakly to distinctly knot-like. Even weakly knot-like trigones will differentiate such collections from *C. semiteres*. I have used differences in trigone magnitude in collections such as these, even though some overlap of characters exists between the varieties. *Engel 13143*, for example, has trigones 6–7.2 μm, and a ratio of trigone diameter to length of intervening thin wall between trigones often less than 1:2 (even though it ranged to 1:2.6). *Chiloscyphus semiteres* has trigones 2.4–4.8 μm, with a ratio of 1:2–5.6 (see Table 9). Populations of *C. canaliculatus* with suboptimal expression of trigones usually occur in shaded, sheltered niches (see Note 1, p. 96). I cannot make a statement regarding branch frequency of sterile shoots in example (1) because the population is exclusively androecial. Presence of androecia does not correlate with a particular branch type, in that shoots with androecia are associated with both terminal and intercalary branches.

Still other collections do not fit into the variation spectrum outlined above. For example, *Engel 18803*, a saxicolous population from South Is., New Zealand, has exclusively lateral-intercalary branching. *Schuster 61672A* from North Is., New Zealand is another example. These very rare phases otherwise clearly fit within the boundaries of the species.

Child 439 from Rees Valley (South Is., New Zealand) is an interesting variant. The plant has well-developed shoot sectors with leaves typical of the species, i.e., with apices undivided and broadly rounded. However, leading shoots sometimes become smaller, and in such sectors the leaves are often retuse-short bifid. Care should be taken in distinguishing such populations from *C. rupicola*, which has accessory teeth on leaves at sites other than lobe positions. *Chiloscyphus canaliculatus* is devoid of such accessory apical and marginal teeth. In this connection it should be remembered that *C. semiteres* also has bifid leaves on suboptimal shoots or shoot sectors.

The student should also be aware of the variation spectrum of two features of *C. rupicola*. Specimens of that species always have at least a suggestion of leaf armature, even in weaker material, and underleaves never have consistently reduced

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Is., Gisborne Prov., Urewera Natl. Park, Waikareiti Track; **5**, from *Engel 22269*, New Zealand, North Is., North Auckland Prov., summit of ridge W of Bream Head.)

lateral armature. In *C. rupicola*, underleaves with tooth-like lateral armature always accompany those with small to large laciniiform processes.

Chiloscyphus canaliculatus is divisible into two varieties that are separable as follows.

Key to Varieties of *C. canaliculatus*

1. Underleaves plane . . . . var. *canaliculatus*
1. Underleaves distinctly concave . . . . var. *concavus*

Chiloscyphus canaliculatus Gottsche, Lindenb. & Nees var. *canaliculatus*

Lophocolea oldfieldiana Steph., Bull. Herb. Boissier 6(9): 790. 1906 (= Spec. Hep. 3: 90), *syn. nov. Chiloscyphus oldfieldianus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 420. 1985 (1984). Type: Tasmania, without specific loc., *Oldfield s.n.*, ex hb. Kew (G!–c. young ♀).

Lophocolea wattsiana Steph., Bull. Herb. Boissier 6(11): 936. 1906 (= Spec. Hep. 3: 116), *syn. nov. Chiloscyphus wattsianus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 425. 1985 (1984). Type: Australia, New South Wales, Richmond River, Minyon Creek, 15 Aug. 1902, *Watts 519* (G!–c. per. + ♂, NSW!–c. per. + ♂).

Underleaves plane to convex.

NOTE—*Lophocolea campbelliana* is an herbarium name cited by Weymouth (1903). The specimen is *C. canaliculatus.*

NOTES ON TYPE SPECIMENS—1) *Jungermannia canaliculata* Hook. f. & Taylor. I have studied several BM and FH specimens of this name collected by Hooker and Colenso. A specimen at FH has androecia, trigonous perianths (but with infolded sides); sporophytes are lacking. The glued specimen is two inches wide, agreeing with the width of the "patch" cited in Hooker and Taylor (1844). Leaf apices may be bidentate-short bifid; these are sometimes on median sectors of shoots, at other times toward the shoot tip. The protologue (p. 563) describes the leaves as "mostly entire, yet toward the top of the stem they shew (sic) a few very indistinct teeth." The protologue states that perianths are bilabiate and "subcompressed previous to the egress of the capsule." The bilabiate shape given surely is due to the infolded sides, and Mitten (1854–55, p. 135) pointed out the discrepancy, stating perianths in the original specimen are actually triquetrous. There is no explicit protologue statement that capsules are present, the above reference to the capsule is the only comment made. It should be pointed out that when capsules occur in other Hooker and Taylor species, these authors often describe a shape (which is lacking in the protologue for this species). I have selected the FH collection as lectotype (Engel, 1992a). Underleaf margins on each side have a dentiform to small laciniiform process. Trigones are distinct and medium and straight sided to large and slightly bulging.

Several apparently authentic specimens were rejected as candidates for a lectotype. A capsule-bearing specimen from BM lacking collector but marked original, New Zealand, and ex hb. Pearson cannot be a lectotype candidate because it lacks androecia (which are described in the protologue) and consists of plants with uniformly entire leaves. The underleaves are ca. 1.5× the stem width, and the lamina on each side has a conspicuous, broad-based, laciniiform to lobuliform projection. Trigones are small and concave sided. The specimen represents a well-developed phase of *C. semiteres*. I also have rejected as lectotype a FH specimen labeled Colenso 392, New Zealand, J. D. Hooker 1843. That collection has sporophytes, but I found no androecia or toothed leaves. The specimen belongs to *C. canaliculatus.*

2) *Lophocolea oldfieldiana* Steph. The specimen represents a well-developed phase of the species. Leaves are undivided and entire-margined, dorsally assurgent and with apices decurved. The dorsal margin is abruptly decurved and forms a cnemis. Underleaves are ca. 1.2× the stem width, and the lamina on each side has a dentiform to small laciniiform process. Trigones are knot-like. Perianths are in the early leaf-fusion stage and included within the bracts.

3) *Lophocolea wattsiana* Steph. The collection consists of sterile and androecial shoots along with those bearing immature gynoecia. Perianths are somewhat exserted beyond bracts and agree with the protologue in shape and mouth characters. Underleaves are small, being ca. 1–1.3× the stem width, and have a dentiform to ciliiform process on each side of the lamina. Trigones are distinctly knot-like.

DISTRIBUTION—Restricted to Australasia: New Zealand: Campbell and Auckland Is., South Is. (sea level–1100 m), North Is. (5–670 m); Australia: Tasmania (sea level–1120 m); Victoria (720–940 m); New South Wales (450–1375 m).

ECOLOGY—This species and *C. semiteres* have a broad ecological amplitude, but differences in moisture tolerances exist. *Chiloscyphus semiteres* is considerably more xeric tolerant, and is rare and sporadic in areas of particularly high rainfall. For example, *C. semiteres* apparently is the only taxon of *Chiloscyphus* that occurs in Western Australia and is particularly abundant in drier areas of Tasmania. The converse exists for *C. canaliculatus*: it is able to tolerate relatively moist sites (e.g., the Tutoko River area mentioned above), but is intolerant of xeric sites. For example, at Smithy Creek (400–500 m, Fiordland Natl. Park), plants occurred on a moist vertical rock face, ca. 50 m above the margin of a stream in a *Nothofagus menziesii* forest with *Weinmannia racemosa* also abundant. At Port Pegasus, Stewart Is., plants formed distinct colonies on bedrock immediately below Belltopper Falls in an open, humid niche dominated by the bedrock, with a forest margin of *Weinmannia racemosa* and *Dracophyllum.* The species also may be subalpine or alpine. At Temple Basin Ski Area (vicinity of Temple and Cassidy basins, Arthur's Pass Natl. Park), plants occurred at ca. 1300–1500 m on soil of a steep slope near an open rocky subalpine stream. In the Mokai Patea Range (W of Ruahine Range) plants occurred as scattered patches, especially in the vicinity of rock outcrops, at ca. 1500 in an area dominated by *Chionochloa* tussock-grassland on predominately south-facing slopes of rocky outcrops and rocky banks with cushion vegetation. Particularly at these high-elevation sites, plants are bright yellowish green, a feature that distinguishes them at several feet distance in the field.

Chiloscyphus canaliculatus is one of the few hepatic taxa that is able to tolerate salt spray and may occur on rocky ledges within the spray zone (see Engel and Schuster, 1973).

SPECIMENS SEEN (selected)—**CAMPBELL IS.:** *Rae s.n.* (CHR); near summit of Mt. Juma, ca. 470 m, *Taylor s.n.* (AK); Col Ridge Fence, ca. 120 m, *Taylor s.n.* (AK); saddle above Lookout Bay, *1960 Expedition s.n.* (CHR). **AUCKLAND IS.:** Ewing Is., *Fineran 1991* as *L. meridionalis* (CHR). **NEW ZEALAND. STEWART IS.:** Port Pegasus, immediately below Belltopper Falls, North Arm, ca. 5 m, *Engel, von Konrat and Braggins 24114* (F). **SOUTH ISLAND. SOUTHLAND:** Bluff Hill, *Allison H 5168*–c. ♂ (CHR); Fiordland Natl. Park, Central Earl Mtns., Mistake Creek, between Triangle Peak and Melita Peak, NE of N end of Lake Te Anau, 740–800 m, *Engel 18803* (F); ibid., N of Te Anau, *Hatcher 1860*–c. per. (F); ibid., S end of Lake Marion, W of Hollyford River, 695 m, *Engel 23161* (F); ibid., Moraine Creek Track, area N of Moraine Creek, W of

Hollyford River, 400–530 m, *Engel 23243*–c. sporo. (F); ibid., Falls Creek, near junction of Hollyford River road and Milford road, *Schuster 67-2423* (F); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18823* (F); Fiordland Natl. Park, Smithy Creek, 400–500 m, *Engel & von Konrat* (F). **OTAGO:** Catlins River area, Papatowai, sea level, *Child H 2942* (F); Berwick, S of Dunedin, ca. 245 m, *Allison H 1352* (CHR); Waipori River, S of Dunedin, *Allison H 1355* (CHR); ibid., above the powerhouse, *Allison H 1346* (CHR); saddle W of road to Mt. Cargill, N of Dunedin, 500 m, *Engel 17552* (F); Mt. Cargill, N of Dunedin, ca. 455 m, *Child H 684* (F); Aramoana (Harbour Entrance), Dunedin, *Allison H 6146* (CHR); Evansdale, near Waitati, N of Dunedin, *Allison H 5224* (CHR); Hindon, ca. 305 m, *Child H 908*–c. ♂ (F); Herbert State Forest, ca. 245 m, *Allison H 1348* (CHR); Pierce Creek, Falls Dam, ca. 610 m, *Child H 852* (F); Paradise, Jordan River, head of Lake Wakatipu, ca. 425–455 m, *Child H 1217* (F); ibid., Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, *Child H 2008* as *L. heterophylloides* (F); Rees Valley, ca. 305 m, *Child H 439* (F); Glendhu Bluff, Lake Wanaka, ca. 305 m, *Allison H 6792* (CHR); Fiordland Natl. Park, Martin's Bay, N of McKerrow River, *Hatcher 1025* (F). **WESTLAND:** Lyttelton Hills, on Bridle Track near Summit Road, *Allison H 6345* (CHR); near township of Fox Glacier, 0.5–0.6 mi. from front of Fox Glacier, *Schuster 48389A*–c. ♂, *60165*–c. per. (F); Westland Natl. Park, Franz Josef Glacier Valley, Roberts Point, SW of Mt. Gunn, ca. 620–670 m, *Engel 18091*–c. per. (F). **CANTERBURY PROV.:** Arthur's Pass National Park, Temple Basin Ski Area, vicinity of Temple and Cassidy basins, ca. 1300–1500 m, *Engel & von Konrat 28516* (F). **NELSON:** Near Salisbury Lodge, ca. 1100 m, *Brown 88/87*–c. sporo. (AK). **MARLBOROUGH:** Pelorus Bridge, *Braggins s.n.* (AK). **NORTH ISLAND. WELLINGTON:** Wairongomai River, *Zotov s.n.* as *L. heterophylloides* (CHR); Tararua Mtns., Ruamahanga Valley, *Zotov s.n.* as *L. heterophylloides* (CHR); ibid., Akatarawa Saddle, *Zotov s.n.* as *L. heterophylloides* (CHR); Ohauiti River, *Zotov s.n.* as *L. heterophylloides* (CHR); Tiritea Stream, *Zotov s.n.* as *L. heterophylloides* (CHR); Ruahine Forest Park, Mokai Patea Range, W of Ruahine Range and NW of Rongotea Peak, ca. 1500 m, *Engel & von Konrat 28156* (F); Western Ruahine State Forest, Oroua Valley, ca. 670 m, *H. Hodgson s.n.* as *L. pallida* (CHR); Tongariro Natl. Park, Mangawhero River near juncture of Rimu Track and Forest Walk, 625 m, *Engel 22713*–c. sporo. + ♂ (F). **HAWKE'S BAY:** Wairoa, "Kiwi," *Hodgson 303* as *L. novaezeelandiae*, *315* (CHR). **SOUTH AUCKLAND:** Kaingaroa Plains, *Allison H 3380* (CHR); E of Waiotapu Valley, ca. 520–550 m, *Allison H 3399* as *L. insularis* (CHR); Rangitaiki River, near Murupara, *Allison H 3465* (CHR); Mt. Ngongotaha, ca. 455 m, *Allison H 3683* (CHR); Okere Falls, NE of Lake Rotorua, *Schuster 67-4380A* (F); Pongakawa River gorge, near Bay of Plenty, *Allison H 637* as *L. novaezeelandiae* (CHR). **NORTH AUCKLAND:** Huia, Manukau, *Brewin s.n.*–c. ♂ (CHR); Waitakere Mtns., Glenness Falls, W of Auckland, *Schuster 51676*–c. per. + ♂ (F); Auckland, *Cheeseman s.n.* as *L. heterophylloides* (STR); ibid., Mt. Wellington Quarry, *Cameron s.n.* (AK); Waitamata Harbour, Rangitoto Is., *Lloyd 30*–c. ♂ (CHR); same loc., ca. 5 m, *Braggins s.n.* (AK); Murray's Bay, *Lloyd 14* (CHR); summit area of Mt. Manaia, NW of Bream Head, SE of Whangarei, 390 m, *Engel 22229*–c. ♂ + per. (F); Whangarei, Otuhi, *McLean s.n.*–c. ♂ (CHR); Waipoua River, ca. 70 m upstream from State Highway 12 bridge, ca. 95 m, *Engel 21051*–c. per. (F); Waipoua Forest, *Allison H 750*–c. sporo. (CHR); Bay of Islands, Russell, Pool's Gully, *Lindauer s.n.* (CHR). **LITTLE BARRIER IS.:** E Cape, *Braggins et al. 80/353*–c. per. + ♂ (AK); E Cape Hut, *Braggins et al. 80/342a*–c. per. (AK). **GREAT BARRIER IS.:** *Kirk s.n.* as *L. heterophylloides*–c. ♂ + per., *151* (CHR). **TASMANIA.** Tasman Peninsula, Port Arthur, Carnarvon, *Weymouth 631* as *L. oldfieldiana* (HO); ibid., W slope of Tatnells Hills, S of Waterfall Bay, 500–530 m, *Engel 13138*–c. ♂ (F); ibid., Waterfall Bay, sea level–150 m, *Norris 27677* (F); ibid., ibid., Camp Falls, 150–240 m, *Engel 12688* (F); ibid., along Block and Stable Creek, at Lake Leake Road, ca. 400 m, *Norris 30692* (F); Storys Creek, above town of Storys Creek, *Norris 32363* (F); W facing slope of Mt. Arthur, Pipers River, NE of Launceston, ESE of Lilydale, 850 m, *Engel 15369* (F); NW facing slope of Mt. Arthur, along track from Mt. Arthur Grammar Hut to Pipers River, NE of Launceston, ESE of Lilydale, ca. 800 m, *Engel 15460* (F);St. Patrick's Head, ca. 610 m, *Weymouth 1246* as *L. geheebii* (HO); St. Mary's Pass, The Glen, ca. 275 m, *Weymouth 1311* as *L. trialata* (F, HO); Launceston, Cataract, *Rodway s.n.* as *L. gunniana* (HO); ibid., Cataract Gorge, *Weymouth 1303* as *L. oldfieldiana*, *1304* as *L. geheebii*, *1305* as *L. macrostipula*, *1306* as *L. subemarginata*, *1308* as *L. forsythiana* (HO); ibid., Trevallyn Creek, *Weymouth 1301* as *L. oldfieldiana* (F, HO, M); Distillery Creek, about 7 mi. E of Launceston, ca. 200 m, *Norris 31677* (F); Mt. Hartz Track, *Rodway s.n.* as *L. spongiosa* (HO); Hartz Mtn. Natl. Park, along trail to Lake Osborne, 900 m, *Norris 29722*–c. per. (F); Watchorn's Hill, Huon Road, near Neika, *Weymouth 523* as *L. fissistipula* (HO); gully below Fern Tree, *Rodway s.n.* as *L. gunniana*–c. sporo. (HO); NW Bay River, ca. 365 m, *Ratkowsky 77/166*–c. ♂ (HO); ibid., *Rodway s.n.* as *L. gunniana*–c. sporo. (HO); Mt. Wellington, ca. 760 m, *Rodway s.n.* as *L. spongiosa*–c. ♂ (HO); ibid., off Pipeline Track, stream course SE of St. Crispins Well, 640–650 m, *Engel 20187*–c. sporo. (F); ibid., Lower Pipeline Track, *Ratkowsky H 1407* (HO); ibid., Deep Creek, *Weymouth 525* as *L. fissistipula* (HO); ibid., McRobie's Gully, *Rodway s.n.* as *L. gunniana* (HO); ibid., plateau, *Rodway s.n.* as *L. rupicola* (HO); Knocklofty, near Hobart, *Weymouth 744* as *L. heterophylloides* (HO); Hobart, Cascades, *Rodway s.n.* as *L. heterophylloides* (HO); Hobart Rivulet, *Curtis s.n.* as *L. campbelliana*, nom. herb. (HO); Proctor's Road, *Rodway s.n.* as *L. forsythiana* (HO); Molesworth Creek, at Big Rocky, ca. 200 m, *Norris 33076* (F); Mt. Dromedary, *Weymouth 846* as *L. bispinosa* (HO); Mt. Field Natl. Park, along Tyenna River, near campground at National Park, ca. 200 m, *Norris 28805* (F); ibid., Mt. Field, ca. 610 m, *Rodway s.n.* as *L. spongiosa* (HO); ibid., just SE of Beatties Tarn, near track to Mt. Field East, 975 m, *Engel 14465*–c. ♂ (F); ibid., Beatties Tarn, 975 m, *Engel 14471*–c. per. (F); ibid., vicinity of track to Lake Seal, near track entrance to Platypus Tarn, 1050 m, *Engel 14432*–c. ♂ (F); The Gap, 11.9 km by road from Gordon River Road, along Florentine Road, WNW of Mt. Tim Shea, E of Lake Gordon, 550 m, *Engel 13596* (F); Victoria Valley Falls, Kenmere Creek, off Victoria Valley Road, 500 m, *Engel 13013*–c. ♂ (F); Derwent Bridge, ca. 700 m, *Norris 28170* (F); Cradle Mtn.–Lake St. Clair Natl. Park, Hugel River, just W of Watersmeet, W of SW end of Lake St. Clair, 760 m, *Engel 14169*–c. ♂ (F); Mackintosh River, at Murchison Highway, *Norris 33769* (F); Great Western Tiers, Walls of Jerusalem Natl. Park, plateau area between Lake Loane and Wild Dog Creek, 1120 m, *Engel 20160* (F); Cradle Mtn.–Lake St. Clair Natl. Park, Pencil Pine Lodge, about 5 mi. N of Cradle Lake campground, *Norris 34158* (F); Lake Lea, ca. 800 m, *Norris 27424* (F); Leven Gorge, along River Leven, 10 km by road from Nietta, SSE of Burnie, 400 m, *Engel 15740*–c. per. + ♂ (F); along Nietta Creek, "Castra Falls," off Gaunts Road, NE of Nietta, 415 m, *Engel 19858* (F); immediately S of Watts Lookout, on road to Upper Castra, ca. 500 m, *Norris 32620* (F). **AUSTRALIA. VICTORIA:** Mt. Elizabeth No. 2, Mt. Elizabeth road via Playground road, 14 km along Omes Highway from Bruethen, ca. 940 m, *Verdon 1186* (CBG); Mt. Macedon–Woodend Road, 6 km ESE of Woodend, 800 m, *Streimann 15485* (F); Bonang River, 59 km NE of Orbost, 720 m, *Streimann 10041*, *10042* (CBG). **NEW SOUTH WALES:** Somersby Falls, near Gosford, *Braggins s.n.* (AK); Carrington Falls, *sin. coll.* (H 177) (NSW); Greenbah Creek, 29 km S of Coonabarabran, 450 m, *Streimann 9479* (CBG); Mt. Boss State Forest, Forbes River, 51 km NW of Wauchope, 1060 m, *Streimann 7151* (CBG); Chaelundi Mtn., 37 km N of Ebor, 1376 m, *Streimann 6719* (CBG); Richmond River, *sin. coll.* (H 203) (NSW); near Ballina, *Watts 492*–c. ♂, *502*, *505* as *L. wattsiana* (NSW); Webster's Scrub, near Ballina, *Watts s.n.* as *L. wattsiana* (M).

Chiloscyphus canaliculatus var. *concavus* J. J. Engel, var. nov.

Varietas in aspectu ventrali amphigastriis distincte concavis praedita.

Holotype—New Zealand, Stewart Is., Fern Gully Track at terminus of Kaipipi Road, Mill Creek, ca. 2 km W of Oban, 20–30 m, *Engel 24081* (F); isotype: (CHR).

Underleaves distinctly concave (ventral view).

Distribution and Ecology—Known only from the type, occurring on rock in a stream bed in a regenerating forest dominated by *Fuchsia excorticata* and *Griselinia littoralis* canopy, with a *Blechnum discolor* understory.

Chiloscyphus fertilis J. J. Engel

Chiloscyphus fertilis J. J. Engel, Phytologia 83: 44. 1998 (1997). Holotype: Australia, New South Wales, Lane Cove, *Forsyth 60* as *L. bridelii*–c. sporo. + ♂ (NSW!).

Plants resembling *C. semiteres* in dorsal aspect, soft, prostrate, pale green; shoots to 2 mm wide. Branches sparing, of lateral-intercalary type; terminal branches not seen. Stems rather narrow for plant size, 7–9 cells high, the cortex poorly differentiated, the cortical and medullary cells very thick walled. Rhizoids in an ill-defined zone from stem at base of underleaves, but not restricted to immediate base of underleaves. Leaves alternate, dorsally assurgent in basal portion, the distal portion broadly to sharply reflexed grading to subhorizontal throughout, occasionally with all or major portion of leaf subvertical; leaves widely spreading, loosely imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip. Leaves often with a broad adaxial concavity, subsymmetrically to symmetrically rather narrowly ovate, 0.95–1.1× longer than wide; apex undivided and entire, broadly rounded to truncate to sporadically feebly retuse; margins entire, the dorsal broadly and slightly rounded, plane to feebly deflexed, short decurrent, the ventral ± curved similarly to the dorsal margin, plane. Leaf cells with walls thin, trigones optimally knot-like and massive (suboptimal plants with trigones weakly knot-like), median leaf cells 24–34 µm wide, 22–30 µm long; surface smooth. Underleaves much smaller than leaves, rather consistent in size, 0.7–1.2× stem width, free or obscurely to distinctly connate on 1 side, insertion occasionally asymmetric, the insertion crescent shaped, the underleaves appressed to slightly spreading, distant to approximate, plane to slightly convex (ventral view), subrectangular to narrowly ovate; apex bilobed to 0.5–0.8 or more by a variably shaped sinus, the sinus at times descending nearly to underleaf base and delimiting a reduced lamina of only 2 cells high; lobes ± parallel to somewhat diverging laterally, acuminate to subcaudate, the lobe margins entire or with 1–2 teeth; lamina margins on each side with a dentiform to ciliiform to laciniiform process, the lamina margins occasionally with an accessory tooth.

Asexual reproduction absent.

Plants dioecious. Androecia on main shoots or elongate, indeterminate lateral-intercalary type branches, the androecia initially terminal but eventually become intercalary, subfolious to subspicate. Bracts somewhat to considerably smaller than leaves, loosely imbricate to rather tightly appressed to bract immediately above, the saccate portion smooth to crenulate in profile and fused toward base with opposite bract, the bracts ventricose in basal portion, the distal portion strongly dorsally assurgent and stiffly vertical to distinctly reflexed and more leaf-like in orientation, the apex as in leaves; lobule margin incurved, with 1–2 ciliiform processes and a few slime papillae; antheridia solitary, the stalk uniseriate. Gynoecia on main shoot or rather long lateral-intercalary branches (with at least a few cycles of vegetative leaves), rarely on *Frullania*-type branches or subfloral innovations; subfloral innovations occasional, from below bracts of innermost series. Bracts of innermost series larger than leaves, often with 1 or both of innermost bracts smaller than bracts immediately below, erect or spreading, often with dorsal-basal sector of innermost bract dilated and ensheathing the dorsal base of perianth, the bracts free from one another, with a broad concavity in basal portion, the shape variable: elliptic to narrowly to broadly ovate to orbicular to feebly obovate; apices plane to ± undulate, rounded to ± truncate to retuse, entire; margins plane or the dorsal slightly reflexed, entire or with 1–2 small dentiform-ciliiform processes. Bracteoles of innermost series much smaller than bracts, 0.2–0.4(0.55)× bract area, free or narrowly to rather broadly connate on 1 side or if connate on both sides, then broad on 1 side and narrow on the other, the bracts plane to slightly concave, ovate to elliptic; apices bifid to ca. 0.1–0.4 by acute to acuminate lobes; lamina margins entire or sparingly dentate and/or laciniiate. Perianth longly exserted beyond bracts, sharply trigonous throughout, clavate to narrowly obovate, the base distinctly narrow-cylindrical, expanding toward the wide, 3-lobed mouth; lobes often tapering to a narrow, rounded to truncate summit, usually undivided, rounded to truncate and entire, or sporadically retuse-bidentate and with a few broad-based teeth, the lobes often repand, sometimes with 1 or 2 of lobes short bifid by entire-margined, broad-acute segments, but never with all 3 lobes bifid; keels sharp, with keelar wings occasional, low, entire or with a few teeth.

Sporophytes commonly present. Seta 8–10 cells in diam., with 24 rows of outer cells surrounding an inner core of scattered cells of similar size. Capsule elliptic, 840 × 630 µm to 1120 × 840 µm, the walls 36–38 µm thick, of 4 (locally 5) layers, the outer layer of cells equal to thickness of 1.8–2 of interior strata; outer layer of cells subquadrate, the radial walls thin, with magenta nodular thickenings mostly on longitudinal walls and less commonly on transverse walls; intermediate and inner layer of cells subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended; innermost layer of cells irregularly short to long rectangular, the walls very thin, with semi-annular bands red brown, narrow, sporadically incomplete, sporadically forked, the radial walls sporadically with nodular to spine-like thickenings.

Spores 11.9–13.5 µm, pale brown, thin, with faint, low, close, papillose and short-vermiculate markings, spore:elater diameter ratio 1.4–1.8:1. Elaters tortuous, 7.7–8.6 µm wide, the spirals 1.9–2.4 µm wide, loosely wound.

DIFFERENTIATION—*Chiloscyphus fertilis* is an ally of *C. semiteres* but may be distinguished from that species by a suite of features. The perianth lobes are undivided and entire (Fig. 38: 11) or have at most two of the lobes short bifid by acute segments. Perianth lobes often markedly taper to a narrow, rounded to truncate summit, a lobe shape not found in *C. semiteres*. However, perianth lobes at times are broadly rounded (Fig. 38: 11), the usual shape for *C. semiteres*. Bracteoles are usually small and only 0.2–0.4× the bract area (Fig. 38: 5–8), whereas those of *C. semiteres* are consistently larger and ca. 0.6 or more the bract area. Sporophytes are nearly always produced, and the specific epithet was chosen to call attention to this character. On the other hand, *C. semiteres* only sporadically produces capsules. Sporophyte presence (and often abundance) is a useful initial clue to the identity of *C. fertilis*.

Some features of the gynoecium are useful taxonomically, but are not universally present. A cylindrieal vestigial stem perigynium is frequently present. The extent of perigynial development is variable, and in some populations the underleaf is elevated to a considerable extent on perigynial tissue. In such cases of vigorous perigynial development the perianth is stout, inflated-trigonous, and nearly cup shaped. A second tendency of the gynoecium is useful taxonomically. The approximate distal half of the perianth decays and the sporophyte protective device is assumed by the calytra, which

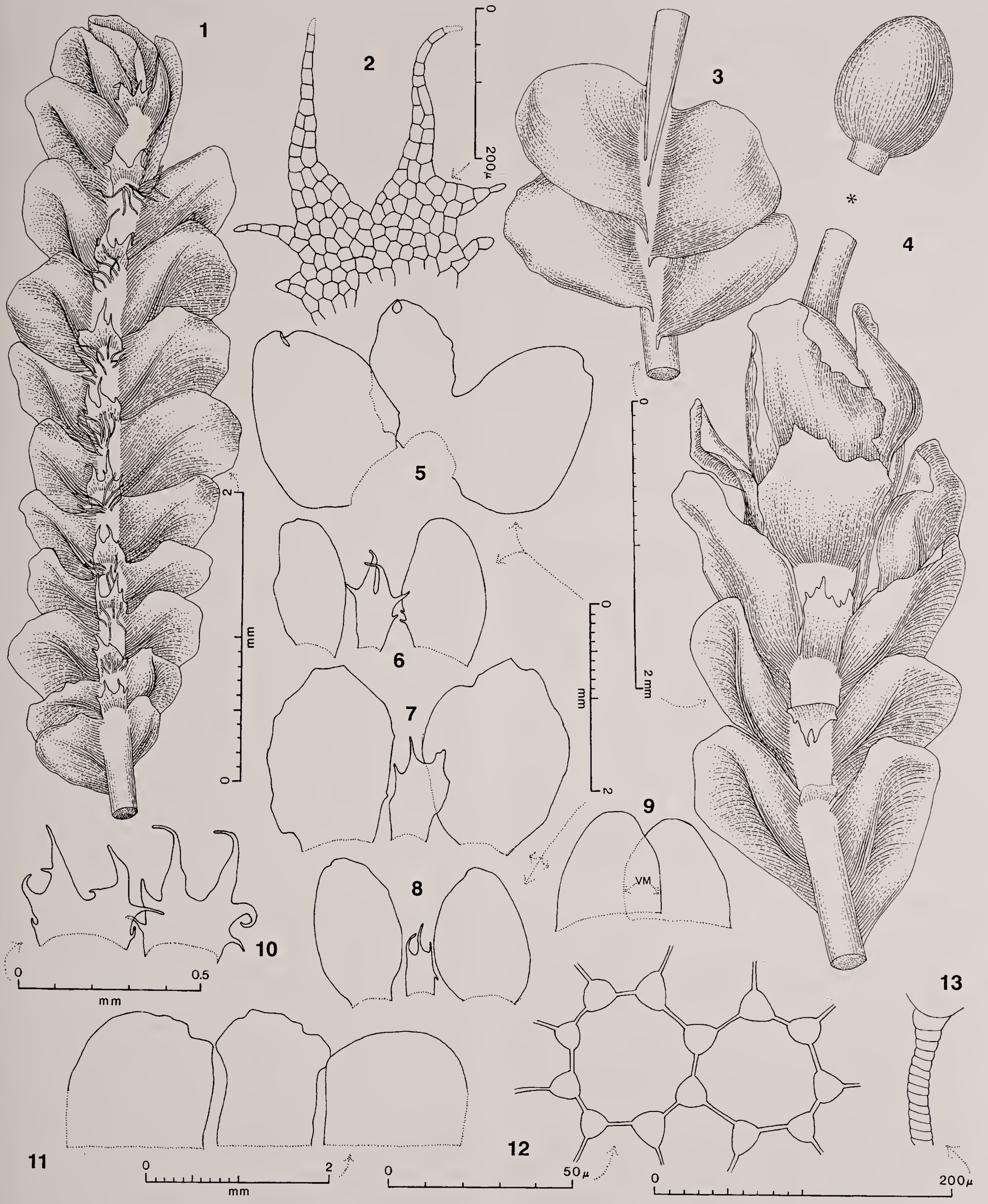

FIG. 38. *Chiloscyphus fertilis* J. J. Engel. **1.** Main shoot, ventral view. **2.** Underleaf. **3.** Main shoot, dorsal view. **4.** Gynoecium with sporophyte, ventral view. **5–8.** ♀ Bracts and in middle, bracteole. **9.** Leaf outlines (vm = ventral margin). **10.** Underleaves. **11.** Perianth mouth, ventral lobe in middle. **12.** Median leaf cells. **13.** Antheridium. (**1–4, 7, 9–11, 13,** from holotype; **5,** from *Watts 856*, Australia, Hopkin's Creek; **6,** from Gore Cove, (*sin coll.*), NSW H 193; **8, 12,** from *Watts 717*, W of Loftus Station.)

remains intact and erect. This phenomenon is apparently unique to the Jungermanniales.

Several features are useful for identification purposes in the few cases when sterile plants are at hand. The species has only lateral-intercalary branches. Underleaves are comparatively narrow, being at most 1.2× the stem width, but are often less wide than the stem (Fig. 38: 1). Trigones are knot-like and when optimally developed are massive (Fig. 38: 12). However, several shoots should be checked for confirmation of the trigone character, especially on shoots with narrow leaves. I have examined several populations, perhaps shade forms, in which some shoots have medium and straight-sided trigones in the leaf middle, but the subapical cells have knot-like trigones.

Characters in the key will separate *C. fertilis* from the allied *C. canaliculatus*, but suboptimal plants present problems. Particularly troublesome are plants that are sterile and sparsely branched, in that the characters used in the key involve these features. Since nongynoecial populations of *C. fertilis* are rare, I have referred such problem specimens to *C. canaliculatus*.

DISTRIBUTION AND ECOLOGY—Known only from Australia (Victoria; A.C.T.; New South Wales, 760 m). The species occurs on shaded, rocky banks of gullies as well as on rock of creek beds.

SPECIMENS SEEN—**AUSTRALIA. VICTORIA:** Buffalo Creek, Gladesville, *Watts 961* as *L. subemarginata*–c. ♂ (NSW); Woodford, *Watts 858* as *L. heterophylloides*–c. sporo. (NSW). **A.C.T.:** Canberra Botanic Gardens, *sin. coll.* (H 173)–c. sporo. (NSW). **NEW SOUTH WALES:** Tomerong, *Watts 620, 621* as *L. bridelii*–c. per. (NSW); Lake George Range, 8 km ENE of Gundaroo, 760 m, *Streimann 4341*–c. sporo. (CBG); Hopkin's Creek, Stanwell Park, *Watts 827* as *L. forsythiana*–c. sporo. (NSW); ibid., *Watts 832*–c. ♂, *854, 856*–c. sporo. + ♂, all as *L. heterophylloides* (NSW); near Loftus, *Watts 713*–c. ♂, *715*–c. sporo., both as *L. geheebii* (NSW); W of Loftus Station, *Watts 717* as *L. forsythiana*–c. sporo. + ♂ (NSW); La Perouse, *Forsyth 50* as *L. bridelii*–c. sporo. (NSW); Balls Head Bay, *sin. coll.* (H 196)–c. sporo. (NSW); Gore Cove, *sin. coll.* (H 193)–c. sporo. + ♂ (NSW); Lane Cove, *Forsyth 29* and *30*–c. sporo., *60*–c. sporo. + ♂, all as *L. bridelii* (NSW); Mosman's Bay, *W. H. P.* (H 183) as *L. heterophylloides*–c. sporo. (NSW); ibid., *sin. coll.* (H 184) as *L. heterophylloides*–c. sporo. (NSW); ibid., *sin. coll.* (H 194)–c. sporo. + ♂ (NSW); Minmi, near Newcastle, *Watts 335* as *L. heterophylloides* (NSW); Alstonville Cutting, 5 mi. from Ballina, *Watts 464* as *L. bridelii*–c. sporo. (FI).

Chiloscyphus rupicola (Steph.) J. J. Engel & R. M. Schust.

Lophocolea rupicola Steph., Bull. Herb. Boissier 6(10): 874. 1906 (= Spec. Hep. 3: 99), *non Lophocolea rupicola* Steph., Spec. Hep. 6: 301. 1922 [New Guinea]. *Chiloscyphus rupicola* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 422. 1985 (1984). Lectotype (*nov.*): Tasmania, River Waratah, Mt. Bischoff, 16 April 1892, *Weymouth 701* (G!–c. sporo. + per.); isolectotype: (HO!–c. sporo. + per.).

Lophocolea insularis Steph., Bull. Herb. Boissier 6(10): 880. 1906 (= Spec. Hep. 3: 105), *syn. nov. Chiloscyphus insularis* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 417. 1985 (1984). Type: New Zealand, Great Barrier Is., *Kirk 335* (G!–c. per. + sporo.).

Lophocolea variabilis Steph., Bull. Herb. Boissier 6(10): 885. 1906 (= Spec. Hep. 3: 110), *syn. nov., non Lophocolea variabilis* Schiffn., Deutsche Südpol. Exped. 1901–1903. 8: 73. 1907 (≡ *Chiloscyphus werthii* J. J. Engel & R. M. Schust.; I. Kerguelen). *Chiloscyphus variabilis* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 424. 1985 (1984). Type: New Zealand, North Is., Mt. Eden, *Kirk 328*–c. per. + ♂, *999* (!).

Lophocolea fissistipula Steph., Bull. Herb. Boissier 6(10): 886. 1906 (= Spec. Hep. 3: 111), *syn. nov. Chiloscyphus fissistipulus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 415. 1985 (1984). Type: Tasmania, on the road from Gardner's Bay to Peppermint Bay Channel, 23 Nov. 1897, *Weymouth 1032* (G!–c. per. + sporo.).

Lophocolea spongiosa Steph., Bull. Herb. Boissier 6(11): 939. 1906 (= Spec. Hep. 3: 119), *syn. nov. Chiloscyphus spongiosus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 423. 1985 (1984). Type: Tasmania, Port Esperance, 8 June 1892, *Weymouth 541* (G!–c. ♂ + per.).

Lophocolea heterophylloides var. *macrocalyx* Pearson, Bull. Misc. Inform. 1924: 68. 1924, *syn. nov.* Holotype: Tasmania, south coast, Recherche (Bay), near Leprena, 18 Jan. 1911, *Weymouth 1525* (BM!–c. per.).

Plants with the general appearance of *C. semiteres*, rather stiff, loosely creeping to slightly ascending, light green, often whitish green in herb.; shoots to 2.6 mm wide. Branches common, normally all or nearly all (95–100%) of lateral-intercalary type, normally rarely and sporadically of *Frullania* type; intercalary branching strictly lateral in position, without tendency toward ventral-lateral placement; half-leaf of terminal branches with same basic shape as leaves. Stems narrow for plant size, 10–12 cells high, the cortex poorly differentiated, the dorsal cortical cells in 1 (locally 2) rows of somewhat larger cells, the ventral cortical cells subequal to the medullary cells or feebly larger, both cortical and medullary cells thick walled. Rhizoids from stem at base of underleaf. Leaves alternate, dorsally assurgent in basal portion, the distal sector broadly to sharply deflexed, widely spreading, imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves completely smooth, without surface ornamentation, with a broad adaxial concavity, weakly asymmetrically to ± symmetrically ovate, often widely so, 1.02–1.3× wider than long, widest at a line bisecting the leaf at 0.2–0.3 from its base; apex variable: undivided, broadly rounded and armed with short, coarse teeth, to, occasionally, short bifid and then the lobes apiculate to subacuminate and terminating in a single cell or a uniseriate row of 2–4(5) ± isodiametric cells with thickened exposed walls, the intervening sinus rounded, often armed; dorsal margin and usually the distal half of the ventral with low coarse teeth or entire, the unarmed leaves variable in frequency: grading from rare or sporadic to rather common (even in same population), but any given shoot with at least a few armed leaves; dorsal margin broadly and gently curved, narrowed at base, deflexed, at times sharply so and forming a cnemis, short to rather long decurrent; ventral margin curvature much like the dorsal, plane. Leaf cells with walls thin, trigones normally knot-like and 6–8.4(9.6) µm in diam., the ratio of trigone diameter to length of intervening thin wall between trigones 1:0.7–2(2.8), the trigones suboptimally medium and straight sided to somewhat bulging but remaining large in volume; median leaf cells 18–23 µm wide × 22–24 µm long to 24–32 µm wide × 30–38 µm long, the cells of lobes and of lamina apex and margins thick walled and with secondary thickenings; median leaf cells commonly dimorphic, mostly thin walled and with trigones, but scattered cells with secondary thickenings, the cells then uniformly very thick walled; surface smooth. Oil-bodies rather large for cell size, dull, opaque, pale grey, 2–6(7) per cell, finely botryoidal, globose to subglobose to elliptic grading to fusiform, less often ovoid, 7.8–8.5 × 5.2–5.9 µm to (more often) 9.1–11.7 × 5.2–6.5 µm to 12.4–14.3 × 5.2–7.2 µm, globose ones 5.2–7.8 µm in diam., subglobose ones 7.8 × 6.5 µm. Underleaves much smaller than leaves, 1.7–2.8× stem width, distinctly but narrowly connate on 1 side and free or sporadically feebly connate on the other, the insertion often asymmetric, crescent to inverted U-shaped, the underleaves slightly to moderately spreading, approximate to feebly imbricate, slightly convex (ventral view), subrectangular to ovate, the apex 2(4)-lobed to (0.5)0.6–0.8(0.9) by a variable shaped sinus, the lamina often reduced and (2)4–5 cells high; lobes ± parallel to somewhat diverging laterally, acuminate to subcaudate, the margins entire or with a few, often opposing teeth; lamina margins plane to slightly recurved, on each side with a process that grades from dentiform to laciniiform to (sporadically) lobuliform (if dentiform, then never predominantly so), the lamina margins otherwise with an accessory tooth near base or entire.

Asexual reproduction absent.

Plants dioecious. Androecia on leading shoots or short to long lateral-intercalary branches, initially terminal but eventually become intercalary, the ♂ branches sometimes appearing to cease growth and then are rather abbreviated, but at times proliferating vegetatively distally (the androecium then basal on a lateral branch); androecia subspicate to subfolious, normally composed of rather few bract pairs (up to 7). Bracts somewhat smaller than leaves, suberect (best seen in lateral view), ventricose and dorsally assurgent in basal half, the distal portion reflexed and at times slightly convex, the saccate portion crenulate in profile and fused toward base with opposite bract, the apices broadly rounded to truncate to sporadically retuse, usually entire, sporadically with a small blunt tooth, the margins entire; lobule small for bract size, the free margin small, inflexed to involute, narrowly rounded and flap-like, crenulate, with slime papillae; antheridia solitary, the stalk of 12–13 cells long, uniseriate or with one vertical cross-wall and then very locally biseriate. Gynoecia dorsally assurgent, on main shoot or lateral-intercalary branches varying from short, abbreviated, and lacking normal vegetative leaves to elongate; subfloral innovations occasional from below bract of third series. Bracts of innermost series much larger than leaves, erect and appressed throughout or appressed basally but distally reflexed and then obliquely to strongly spreading, free from one another, ovate, with a broad adaxial concavity of variable size in basal portion, the distal sector usually convex to canaliculate or sporadically plane; apices undivided and armed with 1 or more blunt to coarse teeth to retuse-bidentate to short bifid; lamina margins plane to reflexed, with several low blunt to coarse teeth. Bracteoles of innermost series subequal to bracts in size to somewhat smaller than bracts, broadly connate on both sides or broadly connate on 1 side and free on the other, concave, subrectangular to wide elliptic; apices bifid to ca. 0.1–0.4 by sulcate, apiculate to subacuminate lobes; lamina margins reflexed, on each with a broad-based laciniiform to lobuliform projection distally, otherwise entire. Perianth longly exserted beyond bracts, sharply trigonous throughout, oblong to elliptic to subclavate, not to feebly narrowing toward the wide, shallowly 3-lobed mouth; lobes broadly rounded, undivided and coarsely dentate to laciniate, the lobes at times shallowly bifid by subacuminate-acuminate, entire segments; keels sharp, with keelar wings sporadic, low, and of several cells high, sparingly armed.

Seta 8 cells in diam., with 26 rows of outer cells surrounding an inner core of scattered cells with corners thickened as in knot-like trigones, the inner cells increasing in size toward middle, the outermost ring smaller than epidermal cells. Capsule elliptic, 910–1015 µm × 665–700 µm, the wall 38–47 µm thick, of 5–6 (locally 7) layers, the outer layer of cells equal to thickness of 2.2–3 of interior strata; outer layer of cells subquadrate, the radial walls with magenta nodular thickenings mostly on longitudinal walls and sporadically on transverse walls; intermediate and inner layers of cells subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended; innermost layer of cells irregular in shape and orientation, basically quadrate to short rectangular, the radial walls with thin continuous sheets of red-brown wall material, with semiannular bands red brown, common, narrow, sometimes incomplete, sometimes forked and sporadically anastomosing to delimit isolated and ill-defined fenestrae.

Spores 11–11.9 µm, pale brown, thin, with faint, low but sharply defined, close papillae and short-vermiculate markings, spore:elater diameter ratio 1.3–1.5:1. Elaters tortuous, 8.2–8.6 µm wide, the spirals 2.4–2.9 µm wide.

DIFFERENTIATION—This species is an ally of *C. semiteres*, and the two are readily distinguishable when optimal plants are at hand. Leaf dentition is the obvious feature that will immediately differentiate the species from *C. semiteres*. However, that feature is not always uniformly expressed throughout a given shoot (see sub Variation), and one must then rely on differences in branching modalities. Weak or depauperate *C. semiteres* may offer problems in that such plants occasionally have retuse to bidentate or even short-bifid leaves (but with position of teeth or lobes typical of divided-leaved hepatics). Other than the teeth constituting the bidentate apex, however, suboptimal *C. semiteres* never has accessory armature at either leaf apex or margins. This constancy of armature position differs from *C. rupicola*, in which one or more teeth have no specific position at the apex, i.e., the apex may have a blunt tooth commonly situated in the median sector or 3–4 scattered teeth. See comments under *C. semiteres*, especially Table 9 (p. 98).

VARIATION—Leaf dentition is the chief variable character of this species. When optimally expressed, teeth are present at the apex, the complete dorsal margin and normally the distal half of the ventral margin (Fig. 39: 3, 9). The basal half of the ventral margin is usually entire, but shoots with copious dentition may have sporadic leaves with a few teeth in that sector. Intrapopulation variability of the character is rather common, wherein some shoots have leaf dentition sparing (Fig. 39: 5, 11) and others have several teeth on all or most leaves (Fig. 39: 11). Populations with shoots predominantly entire leaved must be treated carefully, and search should be made for sporadic expression of the character at the apices of main shoot leaves as well as those of branches. In such populations, dentition is lacking on leaf margins and sparingly expressed on apices.

Short bifid leaves frequently occur in populations with ± optimally expressed leaf dentition; such populations frequently have a combination of bifid leaves and coarsely dentate undivided leaves (Fig. 39: 3). Conversely, reduction in frequency of bifid leaves occurs in populations with suboptimal dentition; at one end of the variation spectrum are plants that completely lack a sinus at the leaf summit.

Perianth lobes are rather variable, even within the same population. Lobes may be undivided and coarsely dentate to laciniate (see Fig. 40: 1, the gynoecium on right side of shoot, and Fig. 40: 3 [lower]) or short bifid (Fig. 40: 1, the gynoecium on left side of shoot, and Fig. 40: 3 [upper]).

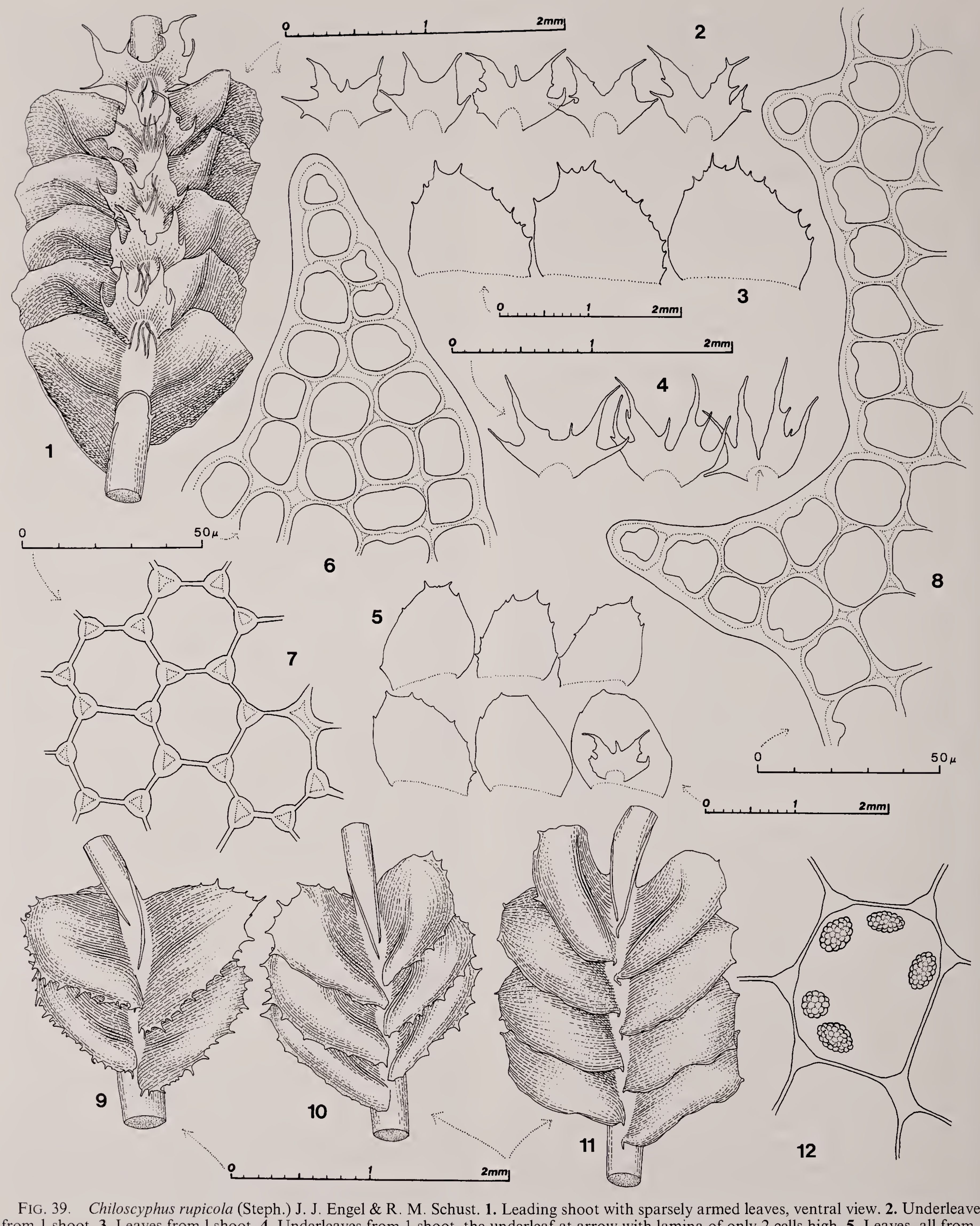

FIG. 39. *Chiloscyphus rupicola* (Steph.) J. J. Engel & R. M. Schust. **1.** Leading shoot with sparsely armed leaves, ventral view. **2.** Underleaves from 1 shoot. **3.** Leaves from l shoot. **4.** Underleaves from 1 shoot, the underleaf at arrow with lamina of only 2 cells high. **5.** Leaves, all from 1 shoot and within, at lower right, an underleaf; note variability of shape, apex and armature; ventral margin at right in top row, at left in bottom row. **6.** Ventral lobe of leaf. **7.** Median leaf cells. **8.** Sector of ventral margin of leaf. **9–11.** Sectors of main shoots, optimally armed leaves (left), rather copiously armed leaves (middle) and rather sparsely armed leaves (right). **12.** Median leaf cells with oil-bodies (900×). (**1, 2, 5–8. 10–12,** from *Engel 20096*, Tasmania, Zeehan-Renison Bell State Reserve; **3, 4,** from *Engel 19762*, Tasmania, Trowutta Caves; **9,** from *Engel 14528*, Tasmania, Kelly Basin Road [Crotty Track].)

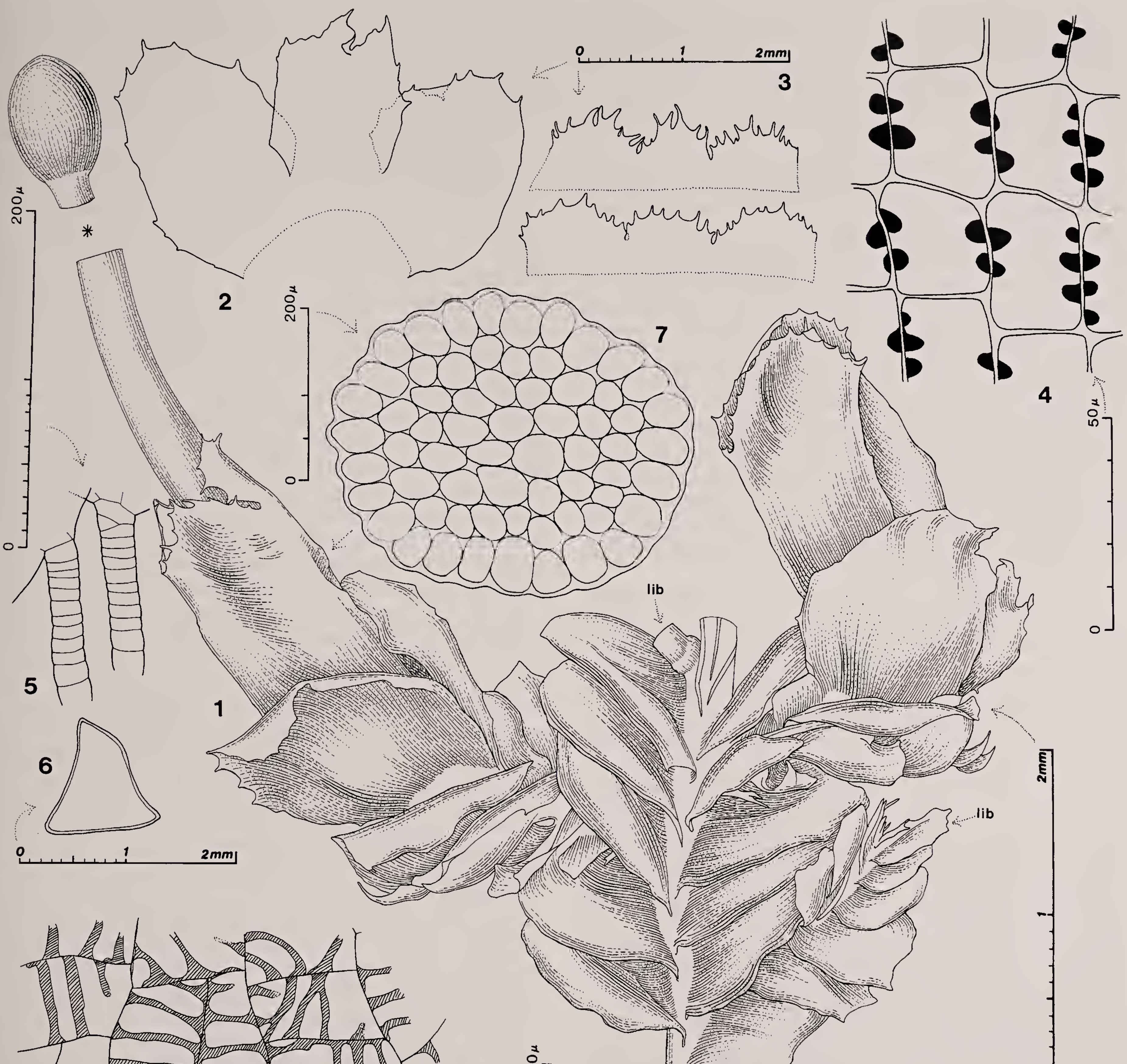

FIG. 40. *Chiloscyphus rupicola* (Steph.) J. J. Engel & R. M. Schust. **1.** Shoot with 2 mature gynoecia on abbreviated lateral-intercalary branches, the gynoecium at left distally has been severed but the position indicated (LIB = lateral-intercalary branch); dorsal view. Note rudimentary wing (at arrow) of perianth at left. **2.** ♀ Bracts and in middle, bracteole. **3.** Perianth mouths, ventral lobe in middle. **4.** Capsule wall, outer layer. **5.** Antheridial stalks. **6.** Perianth, cross section. **7.** Seta, cross section. **8.** Capsule wall, inner layer; note irregularity of cell shape and orientation. **9.** Capsule wall, cross section. (All from *Engel 20096*, Tasmania, Zeehan-Renison Bell State Reserve.)

Note—Several Rodway-collected specimens at HO are misdeterminations of *C. semiteres* and *C. canaliculatus*. This accounts for Rodway (1916, p. 44) stating that the leaf margin of *Lophocolea spongiosa* may be "nude." Rodway was otherwise correct in stating that the leaves may have "a few short broad teeth."

Notes on Type Specimens—1) *Lophocolea rupicola* Steph. The specimen consists of sterile shoots and those that bear immature and mature gynoecia; sporophytes are present. Some shoots have predominantly entire leaves, whereas others are ± regularly and coarsely armed. Leaf apices are broadly rounded to truncate to retuse and may be armed with 1 to several small to coarse teeth. The dorsal margin of the leaf is sharply decurved, forming a cnemis. Dorsal and ventral margins are often sparingly denticulate. Median leaf cell trigones vary from small and concave sided to medium and straight sided to large and feebly bulging. Trigones of subapical leaf cells are more strongly developed and are large and distinctly bulging to ± knot-like. Underleaves are ca. 2–2.8× the stem width, and the lamina on each side has a distinct laciniiform process. Plants have mostly lateral-intercalary branching, but several *Frullania*-type branches also are present. Bracteoles are distinctly connate on both sides but connation is broader on 1 side.

Specimens at G and HO bear the same label information except for number. The specimen at G is number 701, whereas that at HO is 187. The HO collection has the note "Determ'd ipsce autor sub no. 701" and is therefore part of the type collection.

2) *Lophocolea insularis* Steph. Some shoots are variable: certain sectors (primarily basal) have leaves undivided and entire, whereas distal sectors of the shoot have leaves distinctly bifid. Leaves may have a small tooth on the lobes (when present) or at the sinus base, and the dorsal and ventral margins of the leaf are entire or 1-dentate. The underleaves are narrowly connate on one side and free on the other or connate on both sides. Underleaves are bifid nearly to the base, and have the lamina margins on each side with a small to large laciniiform process. Gynoecia are mostly on leading shoots but also may be on short lateral-intercalary branches lacking normal leaves. Trigones are weakly knot-like.

3) *Lophocolea variabilis* Steph. As the name suggests, leaves are variable, the variability chiefly being at the leaf apex. Some shoot sectors are entire-margined and appear strikingly like *C. semiteres*, whereas other shoot sectors have leaf apices 1–2-dentate or short bifid by apiculate to short acuminate lobes. The sinus base may have a tooth, and the dorsal margin is entire or 1–5-denticulate-dentate. Underleaves are distinctly connate on 1 side and free on the other, or narrowly connate on both sides. Trigones are knot-like. Branches are rather common, all of the lateral-intercalary type.

Hodgson (1953, p. 345) mistakenly stated that *Lophocolea variabilis* has surface teeth, an error perhaps based on one of two possibilities. First, a number of collections labeled *Lophocolea variabilis* at CHR and seen by Hodgson are misdeterminations of *C. villosus*, a species with surface teeth. Second, the leaf surface of type material has fungal hyphae which may produce vertical projections. Such projections may have been mistaken for surface teeth by Hodgson. However, I find no indication that Hodgson observed the type.

Two Kirk collections from Mt. Eden, New Zealand, at G bear the orange "typus" label. One, number 328, has numerous shoots, some with androecia, others with perianths (the fertile structures being contrary to the protologue, which indicates the plants are sterile). The other, no. 999, consists of ca. 6 sterile shoots with leaves more copiously armed than most plants in number 328 (some shoots in no. 328, however, are strikingly similar to those of no. 999). Number 999 bears the name "Jack" on the label, and perhaps that collection is a fragmentary segregate of 328 that involves the Jack herbarium.

4) *Lophocolea fissistipula* Steph. Plants consist mostly of shoots that terminate in immature or mature gynoecia; several sporophytes are present. Most shoots have leaf margins entire or sparingly denticulate on the upper ventral and dorsal margins; the leaf apex is often retuse. Such leaves are similar to those described by Stephani as "Folia caulina superiora"; Stephani illustrates such a leaf in his icones (*Lophocolea* no. 162). Stephani also describes "Folia inferiora" and states that these are emarginate-bidentate and have a denticulate sinus and dorsal margin. Such a leaf also is illustrated in Stephani's icone of the species. I have seen only a few shoots that have short-bifid leaves bearing several accessory small teeth, but I have not observed them in lower sectors of shoots. Trigones are variable: some shoots have a mixture of leaves with minute to small trigones and leaves with medium to large and feebly bulging trigones. Basal cells may have weakly knot-like trigones. Underleaves are ca. 2.5–2.8× the stem width, are often asymmetrically inserted and have on each side of the lamina a prominent lacinium or lobule. Both terminal and lateral-intercalary branches are present. The plant represents an extreme of *C. rupicola* characterized by distinct paucity of armature, suboptimal trigone development, and increased percentage of terminal branching. This is perhaps an environmental modification in response to a particularly wet niche with suboptimal light. Increased frequency of terminal branching also occurs in original material of *Lophocolea spongiosa* (*q. v.*).

5) *Lophocolea spongiosa* Steph. The adaxially concave leaves are coarsely dentate at the apex and distal sectors of the dorsal and ventral margins. The dorsal margin is sharply deflexed and forms a cnemis. Trigones are variable: they are medium, straight sided, and small in volume on some shoots and knot-like and ± large in volume on others. Branching is copious, but branch type frequency considerably differs from other populations—terminal branches are about 50% the frequency of intercalary branches (on the basis of the limited number of shoots surveyed). (Plants are not "pauciramosus" as stated by Stephani.) The specimen is somewhat flaccid, trigones are at times smaller, and shoots are large for the species, all suggesting that perhaps the plant occurred in an exceptionally moist niche for the species. Perhaps such a particularly wet niche accounts for the significant increase of terminal branch frequency. The specimen occurred on wood.

6) *Lophocolea heterophylloides* var. *macrocalyx* Pearson. Plants are quite flaccid. Some shoots have leaves that range from those with apices broadly rounded and with a few small teeth to those that are (frequently) short bifid; the sinus margin may be armed. Most shoots, however, have predominantly to exclusively broadly rounded and entire-leaf apices. Trigones are minute to small, the reduced size probably due to the flaccid condition of the plants. The underleaf lamina on each side has a laciniiform to lobuliform process, the large

armature size being somewhat unusual for *C. rupicola*. Most bract apices are short bifid and with several spinose teeth. However, some bract apices are undivided and armed with a few to several spinose teeth. A few bracts are undivided and entire at the apex. I regard the specimen as a sparsely armed extreme, in which dentition is expressed primarily on female bracts and only feebly on leaves.

Distribution and Ecology—New Zealand (North Auckland Prov.); broadly distributed in Tasmania.

In New Zealand the species is restricted to North Auckland Prov. (20–160 m). It is rather common on Rangitoto Is. and occurs on soil over rock in protected niches or on bark of *Metrosideros excelsa*; it may be associated with *Frullania squarrosula*, *Campylopus*, or *Hypopterygium novae-zeelandia*. In Waipoua Forest it occurs on rotten logs in damp and shady niches.

In Tasmania the species is nearly exclusively corticolous, occurring on living as well as decayed wood. It occurs on bark of upright trees, particularly near the bases. It is frequently present on prostrate fallen tree trunks and logs with varying degrees of decortication and decay that range to very rotted, crumbly, decorticated wood on the forest floor. I have frequently encountered the species as scattered small patches quite separated from one another on prostrate, bryophyte-covered, large logs. It also occurs on fallen branches and sticks on the forest floor, suggesting that the plant may be present in the forest canopy. The plant rarely may be found on forest floor litter or over stream bank boulders. It ranges from sea level to 1010 m.

The report by Rodway (1916) of *Lophocolea variabilis* from Tasmania (Mt. Wellington) is based on specimens (2) that are actually *C. subporosus* var. *subporosus*.

Specimens Seen (selected)—**NEW ZEALAND. NORTH ISLAND. NORTH AUCKLAND:** Auckland, *Cheeseman s.n.* as *Lophocolea heterophylloides* (M); Rangitoto Is. 50–160 m, *Engel 20775*–c. per. + ♂ (F); ibid., Waitamata Harbour, 20 m, *Braggins s.n.*–c. ♂ (AK); ibid., Puhutukawa "Is." *Braggins s.n.*–c. per. + ♂ (AK); Waipoua Kauri Forest Reserve, Big Tree Kauri area, *Schuster 67-3807* (F); Waipoua Forest, *Allison H 753* as *Lophocolea variabilis*–c. per. + ♂, *H 1622* as *Lophocolea insularis* (CHR). **TASMANIA.** Tasman Peninsula, Willards Rivulet, *Weymouth 802* as *Lophocolea lauterbachii* (HO); same loc., *Rodway s.n.* as *Lophocolea lauterbachii* (HO); Nelson Creek, at Tasman Highway about 7 mi. W of 1 Buckland, ca. 100 m, *Norris 31122* (F); Storys Creek, above town of Storys Creek, *Norris 32396* (F); Mt. Barrow, ENE of Launceston, 825–930 m, *Engel 15253*–c. per. (F); Mt. Barrow Road, about 3 mi. from top, ca. 800 m, *Norris 31825* (F); Mt. Arthur, NE of Launceston and ESE of Lilydale, 800 m, *Engel 15292*–c. per. (F); St. Columbia Falls, *Norris 32222* (F); Blue Tier, S of Weldborough, ca. 730 m, *Weymouth 1363* as *Lophocolea geheebii* (HO), *1372* as *Lophocolea lauterbachii* (HO, M); Ida Bay, *Rodway s.n.* as *Lophocolea variabilis*–c. sporo. (HO); Port Esperance, *Weymouth 46* as *Lophocolea spongiosa*–c. sporo. (HO); Hartz Mtn. Natl. Park, Mt. Hartz plateau, *Rodway s.n.* as *Lophocolea spongiosa*–c. per. (HO); Arve Valley, Arve Loop Road near junction with Arve Road, N of Hartz Mtn. Natl. Park, 150–200 m, *Engel 12876*–c. per. + ♂ (F); trail from Fern Tree to Silver Falls, 500 m, *Norris 29176* (F); Mt. Wellington, 365 m, *Rodway s.n.* as *Lophocolea lauterbachii* (HO); ibid., St. Crispins (Well), *Weymouth 575* as *Lophocolea spongiosa* (HO); ibid., ibid., 455 m, *Rodway s.n.* as *Lophocolea spongiosa* (HO); ibid., Bower Creek, *Weymouth 18* as *Lophocolea oldfieldiana* (HO); ibid., McRobies Gully, *Rodway s.n.* as *Lophocolea geheebii*–c. sporo. (HO); New Town Rivulet, near Hobart, *Weymouth 895* as *Lophocolea fissistipula* (HO); Mt. Field Natl. Park, Mt. Field, 610–760 m, *Rodway s.n.* as *Lophocolea fissistipula* (HO); ibid., 900 m, *Ratkowsky 78/148* as *Lophocolea semiteres* (HO); ibid., SE of Beatties Tarn, near track to Mt. Field East, 975 m, *Engel 14464* (F); Styx River Road at intersection with Gordon River Road, *Norris 28863* (F); Adamsfield Track in vicinity of Florentine River, W of Mt. Tim Shea and E of Lake Gordon, 400 m, *Engel 13626* (F); Gordon River, Expectation Reach, between Horseshoe Bend and abandoned HEC hut, sea level–50 m, *Engel 14826*–c. per. (F); ibid., ca. 3 mi. from river mouth and Macquarie Harbour, sea level, *Engel 14587*–c. per. + ♂ (F); Lyell Highway near Liapootah Dam turnoff, S of Tarraleah, 520 m, *Engel 12962*–c. ♂ (F); 5 mi. NE of Tarraleah, *Norris 33273* (F); Cradle Mtn.–Lake St. Clair Natl. Park, Pine Valley, between Pine Valley Hut and Cephissus Falls, NNW of Lake St. Clair, 850 m, *Engel 14309*–c. ♂ (F); Surprise Valley, above both Surprise River and Lyell Highway, 2.1 km W of King William Saddle and 17.8 km W of Derwent Bridge, 750 m, *Engel 19449*–c. per. (F); Franklin River near bridge over Lyell Highway, 26 km W of Derwent Bridge, 250 m, *Engel 15015* (F); Kelly Basin Road (Crotty Track), 26.9 km S of Lyell Highway, SSE of Queenstown, 250 m, *Engel 14528*–c. sporo. (F); Zeehan–Renison Bell State Reserve, on Murchison Highway 6.7 km N of intersection with road to Zeehan, 250–320 m, *Engel 20096*–c. sporo. (F); Mt. Read, S of Rosebery, 990–1010 m, *Engel 20035*–c. per. (F); 2 mi. E of Rosebery, *Norris 33663* (F); Mackintosh River, at Murchison Highway, *Norris 33786* (F); Waratah, 610 m, *Rodway s.n.* (HO); Emu (Companion) River near Guildford Road, SSW of Burnie, 500 m, *Engel 15853* (F); Claude Creek, at road from Gowrie Park to Parangana Dam, ca. 600 m, *Norris 32670* (F); waterfalls along Nietta Creek, "Castra Falls," off Gaunts Road, NE of Nietta, 415 m, *Engel 19846*–c. per. (F); vicinity of Trowutta Caves (Arch), 4.5 km by road from intersection of Reynolds Road and Reids Road and 6.9 km from Trowutta Post Office, ca. 180 m, *Engel 19762*–c. per. + ♂ (F); Trowutta, *Rodway s.n.* as *Lophocolea subemarginata* (HO); between Arthur River and Julius River along Sumac Road, S of Roger River West, S of Smithton, 100 m, *Engel 16074*–c. sporo. + ♂ (F).

Chiloscyphus monoicus J. J. Engel & R. M. Schust.

Chiloscyphus monoicus J. J. Engel & R. M. Schust., Nova Hedwigia 39: 419. 1985 (1984) *ut nom. nov. pro Lophocolea floribunda* Steph., Bull. Herb. Boissier 6 (10): 886. 1906 (= Spec. Hep. 3: 111), *non Chiloscyphus floribundus* Steph., Bull. Herb. Boissier 8 (1): 64. 1908 (= Spec. Hep. 3: 240). Type: Australia, New South Wales, North Creek Road, near Ballina, 6 Sept. 1900, *Watts 2688* (G!, NSW!).

Plants with facies of *C. semiteres*, soft, prostrate, and closely appressed to substrate, olive green in herb.; shoots to 1.8 mm wide. Branches common, mostly of lateral-intercalary type, occasionally of *Frullania* type; half-leaf of terminal branches of same basic shape as the leaves. Stems 9–10 cells high, the cortex poorly differentiated, in 1–2 rows of smaller cells, the cortical and medullary cells rather thick walled. Rhizoids in an ill-defined zone from stem at base of underleaves, at times locally scattered. Leaves alternate, often dorsally assurgent in basal portion, the distal portion broadly to sharply deflexed; leaves widely spreading, rather densely imbricate, free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip. Leaves overall convex but with an adaxial concavity in ventral-basal portion, subsymmetrically wide ovate, often as long as wide or slightly longer than wide; apex undivided and entire, broadly rounded to truncate to (sporadically) feebly retuse; margins entire, ± similarly curved, plane, the dorsal short decurrent. Leaf cells with walls thin, trigones medium to large, median leaf cells 20–30 µm wide and long; surface smooth. Leaves bordered by 1–2 rows of smaller cells. Underleaves much smaller than leaves, inconspicuous, often obscured from view by rhizoids, at times disappearing from lower sectors of shoots, ca. 0.7–1.7× stem width, free or narrowly connate on 1 side (both conditions at times on same shoot), the insertion symmetric, crescent shaped, the underleaves appressed to slightly spreading, distant, plane to slightly concave (ventral view), subrectangular to subcuneate; apex bifid nearly to the base, the lamina reduced and of only a few cells high; lobes diverging laterally, acuminate-subcaudate, the

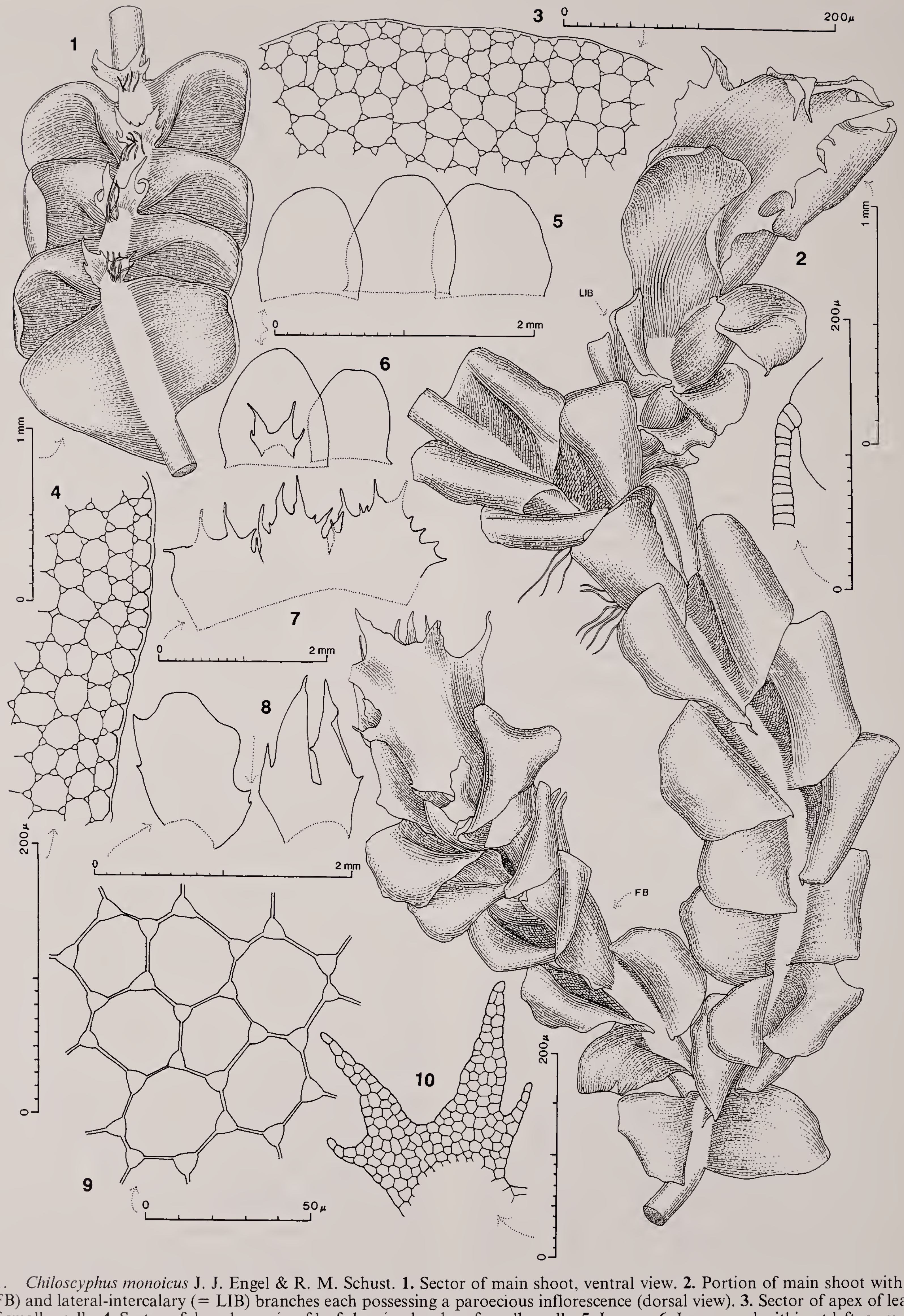

FIG. 41. *Chiloscyphus monoicus* J. J. Engel & R. M. Schust. **1.** Sector of main shoot, ventral view. **2.** Portion of main shoot with *Frullania*-type (= FB) and lateral-intercalary (= LIB) branches each possessing a paroecious inflorescence (dorsal view). **3.** Sector of apex of leaf showing border of smaller cells. **4.** Sector of dorsal margin of leaf showing border of smaller cells. **5.** Leaves. **6.** Leaves and within at left, an underleaf. **7.** Perianth mouth, ventral lobe in middle. **8.** Bract and at right, bracteole, the distal sector of ♂ lobule at arrow. **9.** Median leaf cells. **10.** Underleaf. **11.** Antheridium. (**1–4**, **6**, **9**, **10**, from type; **5**, **7**, **8**, **11**, from *Watts 501*, Australia, New South Wales, near Ballina.)

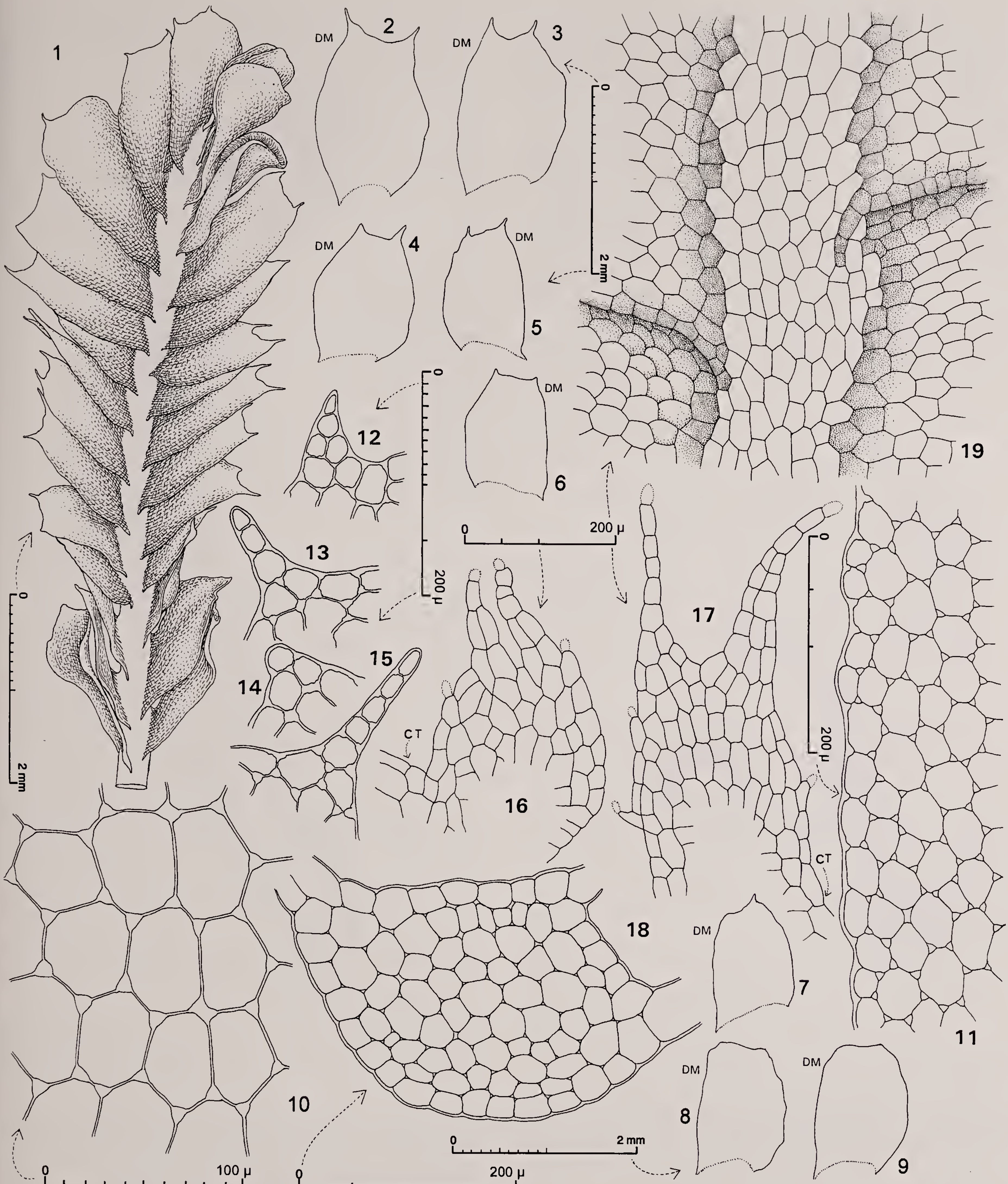

FIG. 42. *Chiloscyphus mediinfrons* J. J. Engel & Braggins. **1.** Portion of shoot (dorsal view); note differences in leaf orientation, spreading distally, becoming dorsally assurgent toward base. **2–9.** Leaves (all drawn to same scale). **10.** Median leaf cells. **11.** Cells of dorsal margin of leaf; note border of smaller cells. **12–15.** Leaf lobes (all drawn to same scale). **16, 17.** Underleaves (CT = connation tissue). **18.** Stem, cross section. **19.** Dorsal surface of stem showing leaf insertion lines and leaf-free gutter. (All from type.)

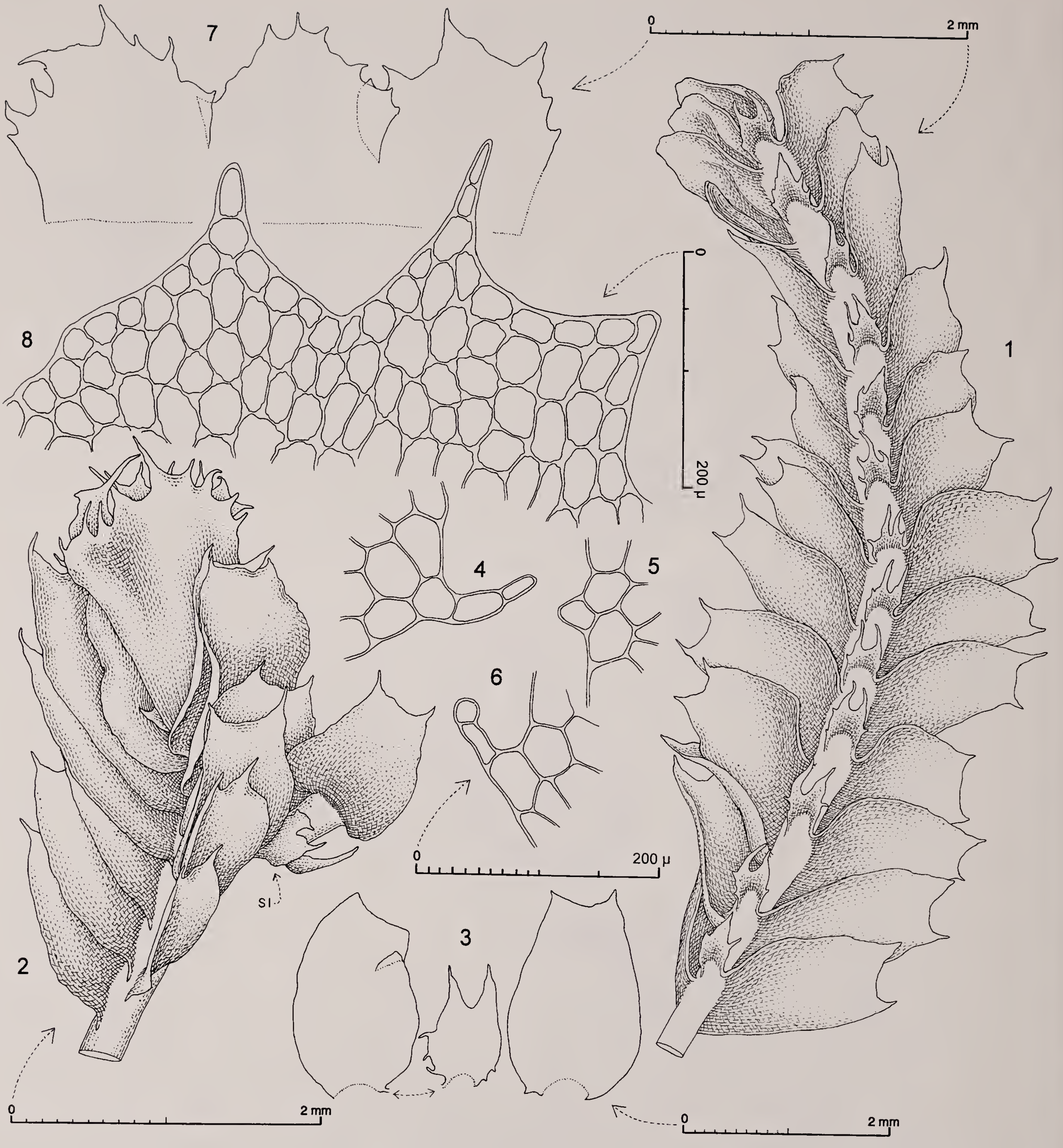

FIG. 43. *Chiloscyphus mediinfrons* J. J. Engel & Braggins. **1.** Portion of shoot, ventral view. **2.** Portion of shoot with perianth, dorsal-lateral view. **3.** Bracts, and in middle, bracteole. **4–6.** Teeth of innermost bracteole disc margin (all drawn to same scale). **7.** Perianth mouth, ventral lobe in middle; note dilation toward lobe bases. **8.** Portion of perianth mouth showing 2 main lobes. (All from type.)

distal sector setaceous, the lobe margins entire; lamina margins on each side with a process grading from dentiform to laciniiform, the lamina margins at times with an accessory tooth.

Asexual reproduction absent.

Plants paroecious. Gametangia produced on main shoots, on short (and lacking normal leaves) to long lateral-intercalary branches or on long *Frullania*-type branches. Androecial bracts in 3–4 pairs, those of innermost series larger than leaves and appearing like normal gynoecial bracts except for development of a lobule. ♂ Bracts with lobule margin incurved, the distal sector of margin grading from a narrowly rounded low projection to a conspicuous, acuminate to parallel-sided, stiffly erect process, the margin otherwise with a small, few-celled tooth and several slime papillae; antheridia solitary, the stalk uniseriate. Gynoecia with vestigial stem perigynium present, narrowly cylindrical, the bracts of innermost 2 series inserted on the vestigial perigynium. ♀ Bracts of innermost series suberect but broadly reflexed distally, subvertical, the apices sometimes canaliculate because of distally revolute margins, the apex variable: mostly rounded to ± truncate, sporadically retuse-1-dentate to retuse-bidentate to (exceptionally) bilobed, the lobes then ventrally sulcate and medium acute; ventral margin entire, occasionally with 1(2) low, broad-based teeth. Bracteoles of innermost series considerably smaller than bracts, free or narrowly connate on 1 side, plane to slightly concave, subrectangular to subcuneate; apices bifid to ca. 0.5–0.7 by plane to ventrally sulcate, acuminate lobes; lamina margins plane or slightly reflexed, entire or with a laciniiform process in vicinity of sinus base (the process may be toward base of outer margin of lobe), rarely with a second tooth. Perianth longly exserted beyond bracts, trigonous throughout or terete in basal sector, clavate to subcampanulate, expanding toward the wide, deeply 3-lobed mouth, the lobes free for ca. 0.5–0.6 the perianth length; lobes deeply bifid, the segments acuminate to subcaudate, entire, the lobes otherwise coarsely dentate to laciniate; keels sharp, especially distally, with keelar wings lacking or low and of a few cells high, unarmed.

Sporophyte not seen.

DIFFERENTIATION—The closest relative of this species is *C. semiteres*, but *C. monoicus* differs from that species in the paroecious inflorescence (Fig. 41: 2), the leaf border of smaller cells (Fig. 41: 3, 4), the often free underleaves, and the more deeply lobed perianths (the lobes free for 0.5–0.6 the perianth length; Fig. 41: 2) with mouth armature more pronounced.

NOTES ON TYPE SPECIMENS—*Lophocolea floribunda* Steph. The original collection, which occurred on tree bark, has leaves nearly always broadly rounded to truncate at the apex. The protologue states the apex may be, though rarely, emarginate-bidentate; I did not observe such apices. The protologue erroneously states that underleaves are free, when actually they are not only free but narrowly connate on 1 side (both conditions at times on 1 shoot). Trigones are medium to large and not small as mentioned in the protologue.

DISTRIBUTION AND ECOLOGY—Known only from Australia (New South Wales), where the species occurs on tree bark and occasionally on sandy banks.

SPECIMENS SEEN—**AUSTRALIA. NEW SOUTH WALES:** East Ballina, *Watts 261* as *L. floribunda*, *264* as *L. heterophylloides*, *275* (NSW); near Ballina, *Watts 499* as *L. bridelii*, *501* as *L. floribunda* (NSW); Alstonville Cutting, 7 mi. from Ballina, *Watts 374* as *L. bridelii*–c. sporo. (FI).

Sect. *Aperticaules* J. J. Engel, sect. nov.

Folia insertione dorsaliter ad lineam caulinam medianam non porrigente, infula cellularum aphyllica praedita. Latitudo amphigastriorum 0.7–1.4-plo latitudinem caulis aequans; amphigastria anguste in latere altero connata et in altero libera vel connata, in aspectu ventrali concava vel canaliculata. Bracteae gynoeciales in apice non divisae vel bifidae usque minores quam 0.1 sui longitudinis. Bracteolae series intimarum aliquantum minores quam bracteae, in apice retusae vel breve bifidae.

TYPE—*Chiloscyphus aperticaulis* J. J. Engel

Plants with stem cortex poorly differentiated. Leaves with insertion not extending to stem midline dorsally, with a leaf-free strip of cells, the insertion not or only feebly recurved at ventral end; leaves with apices undivided and entire (*C. aperticaulis*) or variable and then undivided and 1-dentate to shallowly bifid to occasionally undivided and entire; margins entire. Underleaves 0.7–1.4× stem width, narrowly connate on 1 side and free or connate on the other, concave to canaliculate (ventral view), bifid to 0.2–0.65 by ± parallel or weakly divergent lobes.

Gynoecial bracts of innermost series with an ill-defined cnemis, the apices undivided or bifid to less than 0.1. Bracteoles of innermost series considerably smaller than bracts, the apex retuse to short bifid. Perianth trigonous throughout, expanding toward the wide, 3-lobed mouth, the lobes broadly rounded, shallowly bifid, with accessory teeth below.

This section has two species, both restricted to New Zealand, and occupies an isolated position in subgenus *Lophocolea* in having a conspicuous leaf-free strip of stem cortical cells.

Key to Australasian Species of Sect. *Aperticaules*

1. Leaf apices uniformly undivided, broadly rounded to truncate to weakly retuse; median leaf cells 18–24 μm wide × 20–32(38) μm long; plants pale green, lacking secondary pigmentation; perianth narrowly clavate. New Zealand, North Is., South Is. (Nelson Prov.) . . . . . *C. aperticaulis*
1. Leaf apices variable, undivided and 1-dentate to shallowly bifid, occasionally undivided and completely entire; median leaf cells subisodiametric, 36–42 μm wide × 35–46 μm long; plants pale olive green to pale brown; perianth subcampanulate. New Zealand, Stewart Is. . . . . *C. mediinfrons*

Chiloscyphus mediinfrons J. J. Engel and Braggins sp. nov.

Plantae distincte molles, spongiosae, pallide olivaceo-virides vel brunnescentes. Ramificans perfecte laterali-intercalariter. Insertio folii dorsaliter ad lineam medianam non attingens. Folia ovato-subrectangularia, in apice variabilia, non divisa, 1-dentata vel saepe breviter bifida, interdum non divisa atque integra; sinus truncatus vel lunatus vel late rotundatus; margines folii integrae. Amphigastria aeque lata ac caulis vel angustiora, anguste in latere altero vel utrisque connata, in visu ventrali paulo concava, anguste ovato-subelliptica, bifida usque longitudinis 0.5–0.65; margines laminae dentibus 1–2, sporadice integrae. Plantae dioicae. Gynoecia bracteolis quam bracteis multum minoribus, area bracteolarum ca. 0.35–0.45-plo aream bractearum aequante. Perianthium subcampanulatum, distincte 3-lobum; lobi bifidi, dentibus accessoriis laciniisque praediti.

HOLOTYPE—New Zealand, Stewart Is., Paterson Inlet, Ulva Island, Flagstaff Point, NE end of island, sea level to ca. 60 m, *Engel, von Konrat and Braggins 24598A* (F); isotype: (AK).

Plants strongly anisophyllous, markedly soft and spongy, fragile, brittle, with a waxy appearance, slightly water repellent, loosely creeping to somewhat ascending, pale olive green to pale brown, distinctly nitid when dry, medium, the shoots to 2.6 mm wide. Branching rather common, strictly lateral intercalary, the branches variable in position, from near ventral end of leaf axis, or in axil of leaf–underleaf connation tissue or somewhat apical to this locus, or at lateral edge of underleaf axil, or on ventral-lateral side of axis midway between 2 leaf bases. Stems with cortex poorly differentiated, the cortical cells in a single layer of cells ± similar in size to the medullary or a little smaller, with walls thin; medullary cells thin walled. Rhizoids rather long for shoot size, in fascicles from stem at underleaf bases. Leaves alternate, dorsally assurgent, and often rather strongly so, the distal sector of the leaf gently arched ventrally (the leaves then weakly convex) or the entire leaf stiffly assurgent and with opposing dorsal surfaces of leaf nearly facing one another or, less often, opposing dorsal surfaces juxtaposed and facing one another (in either case the leaves then ± plane), the leaves widely spreading, distinctly imbricate, the orientation strongly succubous, the insertion line straight for the majority of its length before abruptly curving ventrally at the ventral end, which is not or only feebly recurved, the insertion not extending to stem midline dorsally and delimiting a leaf-free strip 4 cells wide; leaves ovate-subrectangular, with apices variable: undivided and 1-dentate to (often) shallowly bifid, occasionally undivided and entire; lobes (when developed) short acuminate grading to apiculate, terminating in a single cell or, more often, a uniseriate row 2–4(5) at most slightly elongated, moderately thick-walled cells, the tip cell tapered to a narrowly rounded to at times rather sharp summit; sinus truncate to lunate to broadly rounded; dorsal margin of the lamina ± straight to weakly and broadly curved, plane or slightly deflexed, uniformly entire, the margin moderately decurrent; ventral margin broadly and gently curved, more strongly curved than the dorsal margin, the curvature symmetrical or more strongly and sharply arched toward the base, the margin plane throughout or reflexed toward base, uniformly entire. Cells thin walled, trigones variable: minute to medium and straight sided to indistinctly bulging, the median cells subisodiametric, 36–42 μm wide × 35–46 μm long; marginal row of cells narrower and often also shorter, forming an indistinct border; surface smooth. Underleaves unistratose, much smaller than leaves, about as wide as stem or somewhat narrower, narrowly connate on 1 side (with nearest leaf base) free or, more often, connate on the other side (with adaxial face of leaf), the insertion crescent shaped; underleaves somewhat distant to contiguous, weakly concave (ventral view), particularly in basal half of lamina, narrowly ovate-subelliptic, typically bifid to 0.5–0.65, the underleaves sporadically unlobed and then acutely tapering distally; lobes slenderly acuminate to subcaudate, at times of differing shape on a given underleaf, the lobes often asymmetrical, subparallel, terminating in a uniseriate row of 2–7, at most, slightly elongated cells, the tip cell capped by a slime papilla, the lobe margins entire; lamina margins on each side with a small tooth comprising 1 cell or a uniseriate row of 2–4 cells, the margin otherwise entire or with an accessory small tooth or slime papilla, the margin sporadically devoid of teeth (but with 1–2 slime papillae).

Plants dioecious. Androecia unknown. Gynoecia on leading shoots or on lateral-intercalary branches with a few cycles of normal leaves or on subfloral innovations with ca. 7 or more cycles of normal vegetative leaves; subfloral innovations frequent, 1–2 per gynoecium; vestigial stem perigynium absent. Bracts crowded, transversely oriented, those of innermost series moderately larger than leaves, erect and ± appressed to perianth, free from one another, overall slightly convex but the basal 0.4–0.6 with an adaxial concavity that "conforms" to the contour of the perianth base, narrowly ovate; apex bifid to less than 0.1, the lobes subequal in size, the segment margins entire; dorsal margin of lamina deflexed and forming a weak cnemis, entire, the ventral margin somewhat undulate, with 1–2 small teeth near base. Bracteoles of innermost series much smaller than bracts (ca. 0.35–0.45× area of bracts), distinctly connate on 1 side, concave toward base (ventral view), narrowly ovate-elliptic; apices retuse-bidentate to bifid to 0.4, the segment margins entire; lamina margins entire or with up to 3 small teeth, the distal one the largest. Perianth moderately exserted beyond bracts, sharply trigonous throughout, the ventral side somewhat to distinctly infolded, the perianths subcampanulate, the sides gradually broadening toward the summit, at times somewhat flared distally, distinctly 3-lobed; lobes broadly rounded, bifid, the segments acuminate to subcaudate, entire, the lobes otherwise dentate to laciniate below level of segments; keels sharp, keelar wings occasional, of a few cells high, entire.

Sporophyte unknown.

DIFFERENTIATION—This species is immediately distinguished from all other members of the genus by the combination of variable leaf apices (Fig. 42: 1–9) and presence of a leaf-free gutter of stem cells (Fig. 42: 19). Leaf apices vary, typically on a single shoot, from undivided and 1-dentate to (often) shallowly bifid to, at times, undivided and entire (Fig. 42: 8, 9). The magnitude of the lobes, whether 1 or 2 on a leaf, also varies. Such variability of leaf apices also is found in *Chiloscyphus novaezeelandiae* var. *novaezeelandiae*, but that plant is much smaller, has leaf insertion lines extending to the dorsal midline of the stem, and often has terminal branching. In nearly all *Chiloscyphus* species the leaf insertion lines attain the stem midline dorsally, and, among our species, the sole exceptions are *C. excisifolius* and *C. aperticaulis*. *Chiloscyphus mediinfrons* differs from all of these species by the smooth, unarmed leaf and stem surfaces and the variable leaf apices. *Chiloscyphus excisifolius* has leaves consistently bifid and *C. aperticaulis* has leaves consistently undivided and entire (and *Cyanolophocolea echinella* has surface echinae on both leaf and stem tissue).

Branching is rather common. Subfloral innovations are very common, and often several are borne from the same gynoecium. One or more of these shoots grow vegetatively for varying distances and either remain sterile or form a gynoecium, which often in turn innovate. These sterile shoots produce only lateral-intercalary branches of varying lengths, which remain sterile or produce a gynoecium.

DISTRIBUTION AND ECOLOGY—Known only from the type, Flagstaff Point, at the NE end of Ulva Is., Stewart Is., New Zealand. Plants occurred with *Zoopsis argentea* and formed a large (ca. 75 × 75 cm) mat on a bank, in forest, under tall *Metrosideros umbellata* and smaller *Weinmannia racemosa*, with seedling *Dracophyllum*, *Metrosideros umbellata*, *Weinmannia racemosa*, and *Coprosma*.

Chiloscyphus aperticaulis J. J. Engel

> *Chiloscyphus aperticaulis* J. J. Engel, J. Hattori Bot. Lab. 95: 229, *f. 1, 2.* 2004. Holotype: New Zealand, North Is., Gisborne Prov., Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20519*–c. per. + ♂ (F); isotype: (AK).

Plants flexuous, loosely creeping to slightly ascending, pale green to pure green, the shoots medium, to 3.2 mm wide. Branching rather common, of lateral-intercalary and *Frullania* types, the frequency variable: some populations with branches nearly exclusively of lateral-intercalary type and with *Frullania*-type branches rare, in other populations with both lateral intercalary and terminal branches, with intercalary branches somewhat more common, still other populations with mostly terminal branches; lateral-intercalary branch position variable: typically from just above leaf–underleaf connation, at times lateral to underleaf lamina, or if lateral-ventral or ventral in position, then originating about midway between two underleaves and never in an underleaf axil, the branch collar high and conspicuous. Stems rather narrow for shoot side, the cortex weakly differentiated, in 1(2) layers of somewhat smaller, thicker walled cells, the exposed wall notably thickened and often pigmented; medullary cells (particularly the outer few rows) with somewhat thickened walls. Rhizoids in loose fascicles from stem at base of underleaves, the rhizoids often dispersed some distance from the underleaf base. Leaves alternate, strongly horizontal, often somewhat dorsally assurgent toward shoot tips, widely spreading, markedly loosely imbricate, free dorsally, the orientation and insertion very broad, strongly succubous, almost longitudinal, forming a nearly straight line in dorsal 0.6–0.9 and then the ventral end varying from slightly and broadly curved ventrally (and not recurved) to sharply but moderately recurved and then J-shaped, the lines of insertion rather distant from stem midline dorsally and delimiting a broad, leaf-free strip of 5–8 cells wide; leaves slightly to at most moderately convex, at times with a weak adaxial concavity in ventral-basal sector, oblate to short oblong-sublingulate; apex undivided and very broadly rounded to (often) truncate to feebly retuse, the apices and margins uniformly entire; dorsal margin broadly and gently curved, or straight up to 0.8 proximally and gently curved distally, the margin plane, at times somewhat deflexed, narrowly rather long decurrent; ventral margin broadly curved (and not more strongly so than the dorsal) to ± straight, the basal extremity of ventral margin at an angle greater than 90° with insertion of median sector of leaf. Leaf cells pentagonal or hexagonal, with walls thin, trigones mostly lacking, sometimes minute, median leaf cells hardly larger than the subapical, being 18–24 µm wide × 20–32(38) µm long; surface smooth. Oil-bodies (2)4–7 per cell, hyaline, broad elliptic to spherical, granular, the granules not perceptibly protruding beyond outer membrane, 6.9–9.8 × 3.9–6.9 µm, spherical ones 4.9–5.9 µm. Underleaves 0.7–1.4(1.6)× stem width, typically narrowly connate on 1 side and long decurrent and free or connate on the other side (thus lower on one side), the underleaves occasionally completely free, but never consistently so on any given shoot, the insertion often somewhat asymmetric, inverted U-shaped but not strongly so; underleaf orientation on same axis often varying from not to hardly spreading to subsquarrose, markedly distant, often separated from one another by at least the length of an underleaf, plane to (often) concave to canaliculate (ventral view), narrowly ovate to subelliptic, the apex variable: short bifid and divided to ca. 0.2–0.3 to (more often) more deeply bifid and divided to 0.5–0.75; lobes ± parallel to feebly diverging, acuminate, often narrowly so, (3)4–7 cells wide at base, often with several biseriate tiers before terminating in a pair of laterally juxtaposed cells or a single cell or, more often, a uniseriate row of 2–4 cells that are uniformly slightly to distinctly longer than wide, the lobe margins entire; lamina margins typically slightly to strongly reflexed, typically on each side with a process grading from dentiform to laciniiform, occasionally with an accessory tooth toward the base.

Asexual reproduction absent.

Plants dioecious. Androecia on leading shoots or elongate lateral-intercalary branches, the androecia subfoliose and only slightly narrower than sterile portions of shoot; bracts in up to 8 pairs, similar to vegetative leaves in shape but somewhat smaller, the bracts ± obliquely oriented (and thus differing in orientation from leaves), at most feebly dorsally assurgent, very weakly imbricate, the saccate portion free from opposing bract, the remainder of bract slightly convex, the apex and ventral margin entire; lobule well defined, small for bract size, rather elongate, the margin free only at upper end of the lobule, "flap-like," and incurved over the opening of the pouch, the margin with 1–2 broad acute teeth; antheridia 1 per bract, the stalk to 17 cells long, uniseriate. Gynoecia on main shoots and long subfloral innovations. Bracts almost plagiochiloid in appearance because of strongly and sharply decurved dorsal margins, an ill-defined cnemis present, the bracts of innermost series free from one another, suberect to obliquely spreading, not ensheathing the perianth base, convex, often canaliculate toward the apex because of distally revolute margins, the bracts slightly asymmetrically broad ovate-orbicular to subelliptic, the dorsal margin slightly longer than the ventral; apex plane or undulate, broadly rounded to truncate to feebly retuse, entire or repand or (sporadically) with a low, broad-based tooth; dorsal margin entire, the ventral margin often undulate, uniformly entire. Bracteoles of innermost series considerably smaller than bracts, free or narrowly connate on 1 side, concave (ventral view), broad elliptic; apex retuse to short bifid, the segments broad and tapering to a narrowly rounded summit; lamina margins reflexed, entire. Perianth longly exserted beyond bracts, trigonous throughout, narrowly clavate, expanding toward the wide, 3-lobed mouth; lobes broadly rounded, shallowly bifid, the segments broad and tapering to a narrowly rounded summit, the segment tips occasionally ± apiculate, the lobes otherwise with a few broad-based teeth below the level of the segments; keels sharp, with keelar wings lacking or low and of a few cells high, entire or with a few small teeth.

Sporophyte not seen.

DIFFERENTIATION—This is the only Australasian *Chiloscyphus* species with consistently undivided leaf apices and a leaf-free gutter (Fig. 44: 2, 3). Additional characters useful in identification of the species nearly all involve the underleaf: typically connate on 1 side (Fig. 44: 1), often deeply divided (bifid to 0.75), and the lamina on each side has a process grading from dentiform to laciniiform (see Figs. 44: 7; 48: 4). The dense areolation of the leaves is also distinctive (Fig. 46: 3). Leaf cells are small (18–24 µm wide × 20–32 µm long) and have thin walls with trigones absent or at most minute (Fig. 44: 6).

The concept of *Lophocolea planiuscula* sensu Hodgson (1953) apparently included elements of both the type, *Jungermannia planiuscula*, and the species described above as *C. aperticaulis*. The true *L. planiuscula* was transferred to *Heteroscyphus* (Engel, 1990b) and occurs on Auckland Island and South Is. as well as North Is., New Zealand. The description in Hodgson (1953) applies mostly to *Chiloscyphus aperticaulis* (the androecia, described by Hodgson as having "bracts spreading, entire," are very likely referable to a *Chiloscyphus*). Also, Hodgson (1953) cites many specimens from North Is., in addition to a relatively few from South Is. Moreover, North Is. specimens from the Allison herbarium (often named or verified by Hodgson) at CHR bearing the name *Lophocolea planiuscula* are all *C. aperticaulis.*

Chiloscyphus aperticaulis and *H. planiusculus* are strikingly similar in the vegetative condition. Both have undivided, entire leaves that are broadly rounded to truncate at the apex, and with a broad insertion that does not reach the stem midline dorsally, a leaf-free gutter of stem cells ensuing. Both have small underleaves, often narrowly ovate, concave, and of

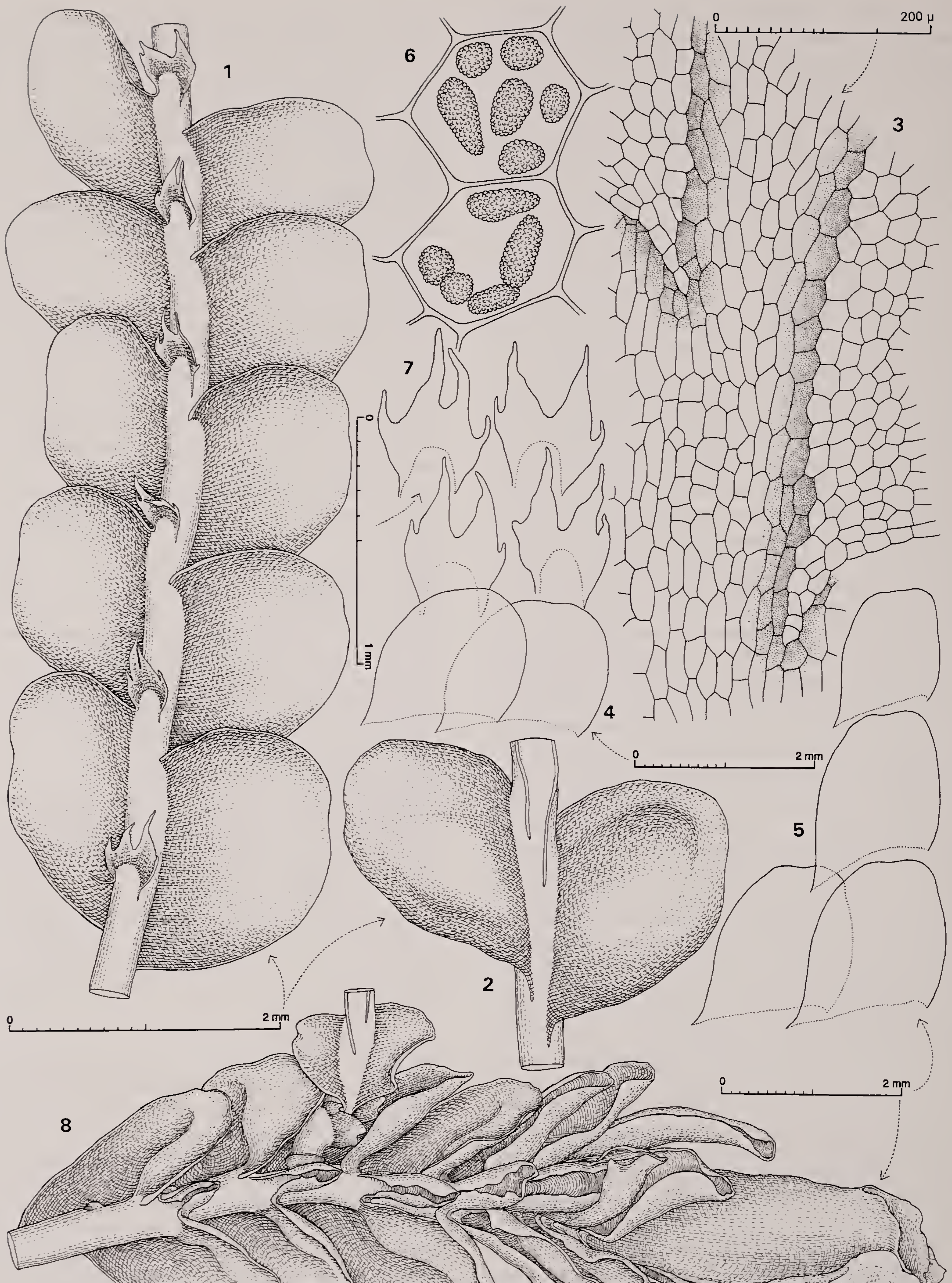

FIG. 44. *Chiloscyphus aperticaulis* J. J. Engel. **1.** Portion of main shoot, ventral view. **2.** Leaf pair, dorsal view. **3.** Dorsal surface of stem showing leaf insertion lines and leaf-free gutter. **4, 5.** Leaves. **6.** Median leaf cells with oil-bodies (1655×). **7.** Underleaves. **8.** Portion of main shoot with gynoecium (ventral view); note the markedly canaliculate bracteoles and underleaves, and the 180° reversal of symmetry of the lateral-intercalary branch. (**1–4, 6–8,** from type; **5,** from *Engel 20810*, New Zealand, North Auckland, tributary of Mangamuka River, Maungataniwha Range.)

about the same width as the stem or a little narrower. Sterile plants of *C. aperticaulis* and *H. planiusculus* may be distinguished in the key below.

Lophocolea planiuscula sensu Hodgson also included *Chiloscyphus austrigenus*. For example, specimens from the Allison herbarium (often determined or verified by Hodgson) at CHR determined as *Lophocolea planiuscula* from the South Is. are mostly *C. austrigenus. Chiloscyphus aperticaulis* and *C. austrigenus* are in several respects similar (e.g., the undivided leaves with apices broadly rounded to truncate, the concave underleaves, connate on one side), and previous confusion therefore is not surprising. Moreover, the two species have a similar ecology, both frequently occurring over rock of stream beds. These two species differ by several characters, as seen in the key below. Moreover, the distribution of these species within New Zealand is completely different: *C. austrigenus* is primarily a South Is. plant and is present on North Is. only at upper elevations (1370–1495 m), whereas *C. aperticaulis* is nearly exclusively a North Is. species and occurs at lower elevations (60–920 m).

Key to *C. aperticaulis* and Similar-Appearing Species

1. Leaf insertions extending to stem midline dorsally, a leaf-free strip of stem cells lacking 2
   2. Underleaves much wider than the stem (to 3.7× stem width), with apices varying from retuse-bidentate; leaf cell trigones mostly small to medium, occasionally large to bulging . . . . *C. austrigenus*
   2. Underleaves narrower than stem; leaf cell trigones usually absent or small . . . . *Clasmatocolea vermicularis*
1. Leaf insertions not extending to stem midline dorsally, a leaf-free gutter of stem cells present; underleaves at most 1.4× stem width and bifid up to 0.75 3
   3. Ventral margin of leaf broadly curved to ± straight, uniformly entire (Fig. 44: 4, 5); median leaf cells small, 18–24 µm wide × 20–32(38) µm long; branching often predominantly lateral intercalary (Fig. 45: 2); underleaves ± symmetrically lobed, the two lobes ± similar in form (Figs. 44: 7; 45: 4); androecia on leading shoots, with ♂ bracts ± leaf-like (Fig. 45: 2) . . . . *C. aperticaulis*
   3. Ventral margin of leaf dilated and subauriculate in basal sector (well-developed leaves), at times with a tooth or slime papilla; median leaf cells larger, 28–40 µm wide × 32–42 µm long; branching mostly of *Frullania* type; underleaves often asymmetrically lobed, the lobes of differing size and configuration; androecia on abbreviated, determinate, lateral-intercalary branches, subspicate . . . . *Heteroscyphus planiusculus*

VARIATION—Although the leaves are for the most part consistent in form, the underleaves often are quite variable. Orientation ranges from ± parallel with the stem to subsquarrose, often on a single shoot. Concave underleaves are usually moderately to strongly spreading, and plane ones not or hardly so. The sinus may be short bifid and divided to ca. 0.2–0.3, a condition that often occurs in the distal portion of the shoot. More deeply divided underleaves are more common; these are bifid to 0.5–0.75. The lamina margin typically has a process on each side that is variable in size. It may be a mere few-celled, blunt projection or a sharp, small tooth or a small to large laciniiform process (Figs. 44: 7; 45: 4).

Differences in development may be observed as a correlation relating to proximity to water. For example, at the Mangamuka River site, plants are ± optimal when just above water level compared with suboptimal when 3–4 feet above water level.

DISTRIBUTION AND ECOLOGY—Endemic to New Zealand, this species is known from scattered sites on North Is., ranging from near Wellington north to North Auckland Prov.; also known from a few sites in the north of South Is. (Nelson Prov.).

The species occupies a distinct and rather narrow ecological niche and occurs over rock in clear, rapidly flowing streams in shady sites. It is found both at the summit of stream bed rocks just above water level in niches that are subject to inundation or, less often, permanently submerged in 2–4 inches of water. It has also been found on a bryophyte-covered vertical bank of the spray zone of a waterfall (here plants grow at nearly right angles to the substrate), the site permanently moist or inundated, and surrounded by mature *Melicytus ramiflorus* forest (180 m, Waitanguru Falls, *Engel 23803*). At lower elevations (below 200 m) the species occurs in mixed broadleaf forests such as those dominated by *Beilschmiedia* and *Vitex* and with nikau (*Rhopalostylis*), *Coprosma*, *Dacrycarpus*, and *Hoheria* also present (Kiwanis Reserve). At upper elevations (650–920 m), the species may be found in *Nothofagus–Dacrydium cupressinum–Podocarpus totara* forests (type). Also, at Garibaldi Ridge in the vicinity of Gordon's Pyramid (Kahurangi Natl. Park, Western Nelson), the species occurred at 1335 m over soil under grass at the side of the bank of a large karst system, ca. 50 m long, narrow, and to 10 m deep, set in a karst plateau landform including large and open trenches and erosion holes, with the vegetation dominated by tussockland, grassland, and herbfields, including *Dracophyllum rosmarinifolium*, *Chionochloa pallens*, and *C. australis*.

SPECIMENS SEEN (selected)—**NEW ZEALAND. SOUTH ISLAND. NELSON:** Kahurangi Natl. Park, Garibaldi Ridge, vicinity of Gordon's Pyramid, 1335 m, *Engel and von Konrat 27098* (F); Maitai Valley, Maitai Cave Track S of Maitai Valley Road and Maitai dam, ca. 240–285 m, *Engel and von Konrat 28226* (F); Mt. Arthur, *Sainsbury s.n.* (Hodgson no. 246)–c. ♂ as *L. planiuscula* (CHR). **NORTH ISLAND. WELLINGTON:** Near Wellington, *Kirk 477* as *L. planiuscula* (CHR); Otupae, Taihape, *A. Hodgson* (ex hb. E. Hodgson no. 616) as *L. planiuscula* (CHR). **HAWKE'S BAY:** Dannevirke, ex hb. Colenso no. a1698 as *L. planiuscula* (CHR); "Kiwi," near Wairoa, 1929, *Hodgson 3*, *99*, both as *L. planiuscula* (CHR); Mahia Peninsula, *Hodgson 395* as *L. planiuscula*–c. ♂ (CHR). **GISBORNE:** Waikaremoana, 1929, *Hodgson 12* as *L. planiuscula* (CHR). **SOUTH AUCKLAND:** Kaingaroa Plains, Rotorua Region, Run 95, *Allison H2210* as *L. planiuscula* (CHR); Harakeke Stream, near Atiamuri, S of Rotorua, *Allison H3706* as *L. planiuscula* (CHR); Waitanguru Falls, Mangaotaki Catchment, Waitanguru Scenic Reserve, 180 m, *Engel 23803* (F); Coromandel Peninsula, Port Charles, *Moore H106* as *L. planiuscula*–c. young ♀ (CHR). **NORTH AUCKLAND:** Mangamuka River, Mangamuka Gorge Scenic Reserve, S side of Maungataniwha Range, near Soda Spring, 5 km W of Mangamuka township, ca. 120–140 m, *Engel and von Konrat 27595* (F); tributary of Mangamuka River, Maungataniwha Range, SE of Kaitaia on State Highway 1, 200 m, *Engel 20810* (F); Kiwanis Reserve, junction of Okahu Stream and unnamed stream, ca. 5 km S

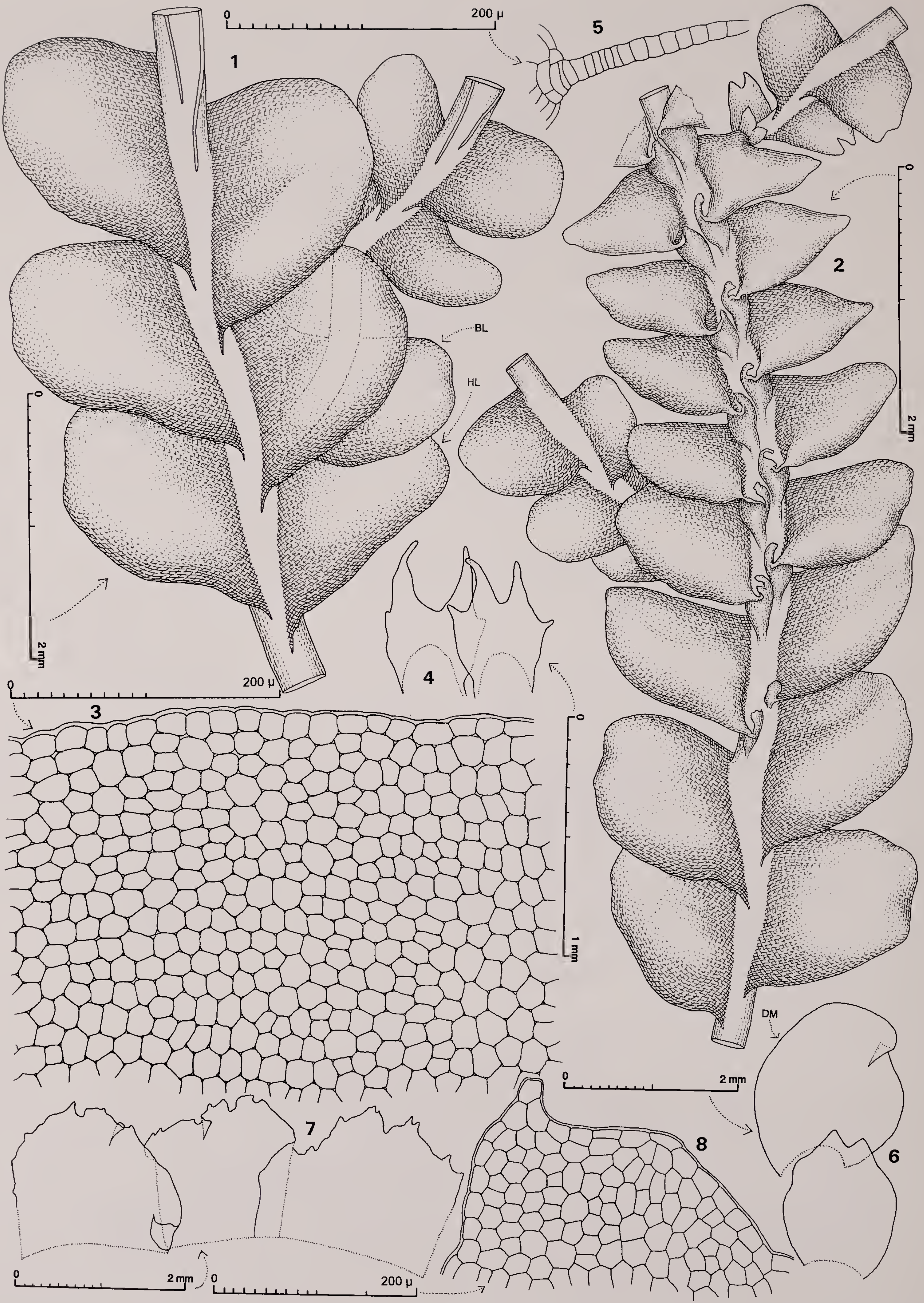

FIG. 45. *Chiloscyphus aperticaulis* J. J. Engel. **1.** Portion of main shoot with *Frullania*-type branch, dorsal view (bl = branch leaf; hl = half-leaf). **2.** Portion of main shoot showing sterile leaves toward base and ♂ bracts distally (dorsal view); note also bases of 2 lateral-intercalary branches, the branch at left long, leafy, and with an androecium terminal in position. **3.** Median-distal portion of leaf showing small cells and dense areolation. **4.** Underleaves. **5.** Antheridial stalk. **6.** Innermost ♀ bract (dm = dorsal margin) and below, bracteole. **7.** Perianth mouth, ventral lobe in middle. **8.** Segment of perianth lobe. (**1–3, 5–8,** from type; **4,** from *Engel 20810*, New Zealand, North Auckland, tributary of Mangamuka River, Maungataniwha Range.)

of Kaitaia, N edge of Herekino Forest area, S of Quarry, ca. 60–80 m, *Engel 20924* (F).

Subg. *Septati* J. J. Engel, subg. nov.

Ramificans saepissime laterali- atque ventrali-intercalariter; ramuli terminales raro praesentes. Rhizoidea septata et non septata. Insertio folii valde succuba, in aspectu dorsali ad lineam caulinam medianam attingens. Folia non divisa atque integra. Stipes antheridialis irregulariter multi-seriatus (usque 6-seriatus).

TYPE—*Chiloscyphus septatus* J. J. Engel.

Branching nearly always lateral- and ventral- intercalary; terminal branches rare. Rhizoids both septate and nonseptate. Leaves with insertion strongly succubous, extending to stem midline dorsally; leaves undivided and entire. Underleaves as wide as stem or a little narrower, very narrowly connate on 1 side and free on the other, concave (ventral view), occasionally plane. Antheridia stalk irregularly multiseriate (6-seriate).

This monotypic subgenus, restricted to New Zealand, is unique in the genus in having septate rhizoids and multiseriate antheridial stalks.

Chiloscyphus septatus J. J. Engel, sp. nov.

Ramificans saepissime laterali- atque ventrali-intercalariter; ramuli terminales raro praesentes. Rhizoidea septata et non septata. Insertio folii valde succuba, in aspectu dorsali ad lineam caulinam medianam attingens. Folia non divisa atque integra, trigonis cellularum foliarium minutis; cellulae folii medianae 24–34 µm latae × 35–42 µm longae. Stipes antheridialis irregulariter multi-seriatus (usque 6-seriatus).

HOLOTYPE—New Zealand, North Is., North Auckland Prov., Radar Bush, WSW of Cape Reinga, S of Mt. Te Paki, ca. 100 m, *Engel 20825*–c. ♂ (F); isotype: (AK).

Plants soft and flexuous, loosely creeping to weakly ascending, the distal portion of shoot occasionally with small and distant leaves but not flagelliform and with scale-like leaves, the plants pale olive green, nitid when dry, the leafy shoots to 2 mm wide. Branches rather sparing, nearly exclusively of lateral- and ventral-intercalary types; lateral-intercalary branches variable in position: ventral-lateral between 2 underleaves, at times ventral lateral and at base of an underleaf on the side opposite underleaf–leaf connation, still others in the axil of underleaf–leaf connation; ventral-intercalary branches common, the collar high; terminal branches rare (only 2 seen). Stems with cortex moderately differentiated, in a single layer of smaller cells with walls slightly thickened; medullary cells thin walled. Rhizoids colorless, in rather tight fascicles at immediate base of underleaves, but at times scattered in an ill-defined region and not at immediate base of underleaf; rhizoids of 2 types: some narrow, 13–18 µm wide and nonseptate (but at times with peg-like swellings of the interior wall), the rhizoid tips often branched, but other rhizoids wider, 26–36 µm wide and regularly septate, occasionally branched, the branches below the tips. Leaves rather stiff, alternate, weakly dorsally assurgent, widely spreading, loosely imbricate, free dorsally, the orientation and insertion strongly succubous, the insertion slightly recurved at ventral end and distinctly oblique in dorsal half, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells; leaves plane to weakly convex, ± symmetrically orbicular to oblate; apex undivided and very broadly rounded to truncate to sporadically feebly retuse, the apices and margins uniformly entire; dorsal margin broadly and gently curved, plane, not decurrent; ventral margin broadly curved, the curvature similar to the dorsal, plane. Leaf cells with walls thin, trigones minute, median leaf cells 24–34 µm wide × 35–42 µm long; surface smooth. Underleaves rather inconspicuous, 0.8–1× stem width, very narrowly connate on 1 side (by 1 cell or part of a cell) and free on the other, the insertion symmetric, ± crescent shaped; underleaves moderately to strongly spreading, distant, somewhat concave (ventral view), occasionally plane (particularly toward the shoot apex), narrowly ovate, the apex bidentate varying to bifid to at most 0.35; lobes ± parallel to slightly diverging, acute to acuminate, typically terminating in a uniseriate row of 2–3 cells that are about as long as wide, the lobe margins entire; lamina margins plane or slightly reflexed, entire or with a tooth variable in position.

Asexual reproduction absent.

Plants apparently dioecious. Androecia rather commonly produced, on main shoot or moderately to distinctly elongate, indeterminate, ventral-intercalary branches, the androecia initially terminal but eventually become intercalary, subfoliose to subspicate. Bracts moderately to distinctly smaller than leaves, erect to suberect throughout and then subvertical, or the basal, saccate portion suberect and the distal portion reflexed, the bracts dorsally assurgent, loosely to rather closely imbricate, the saccate portions of opposing bracts fused toward base or free, the apex and ventral margin entire; lobule free margin inflexed, with a dilated flap that is truncate or rounded at the summit (or at times with 2 flaps separated by a shallow sinus), the margin of the flap(s) entire or with a slime papilla; antheridia solitary, the stalk irregularly multiseriate (?always 6-seriate). Gynoecia not seen.

DIFFERENTIATION—The new species at first glance resembles *Stolonivector waipouensis* J. J. Engel, a plant known only from the Waipoua River in North Auckland Prov., New Zealand (see Engel, 2003). The two species both have undivided, entire, ± orbicular leaves that are inserted to the stem midline dorsally and also small underleaves that have apices bidentate to short bifid. These characters are also present in *Clasmatocolea vermicularis* (Lehm.) Grolle, a pan-south temperate species (see Engel, 1980), with which both of these taxa may be confused. The three species may be separated by the following key.

Key to *C. septatus* and Similar-Appearing Species

1. Leaves weakly to distinctly concave; underleaves typically free; branching terminal, or if intercalary, then mostly ventral . . . . . . *Clasmatocolea vermicularis*
1. Leaves plane to convex; underleaves narrowly connate on 1 side; branching always intercalary or nearly so, with both lateral- and ventral-intercalary branches common . . . 2
    2. Stolons lacking, the leafy shoots not becoming flagelliform; septate rhizoids present; dorsal margin of leaf not decurrent; leaf cell trigones minute, with median leaf cells more elongate, 24–34 µm wide × 35–42 µm long . . . . *Chiloscyphus septatus*
    2. Stolons present, the leafy branches often cernuous and becoming flagelliform; septate rhizoids lacking; dorsal margin of leaf long decurrent; leaf cell trigones medium and straight sided, with median leaf cells nearly isodiametric, 16–24 µm wide × 17–26 µm long . . . . *Stolonivector waipouensis*

The species has two types of rhizoids. Some are narrow, (13–18 µm wide), nonseptate, and sometimes have peg-like swellings of the interior wall, with the rhizoid tips often

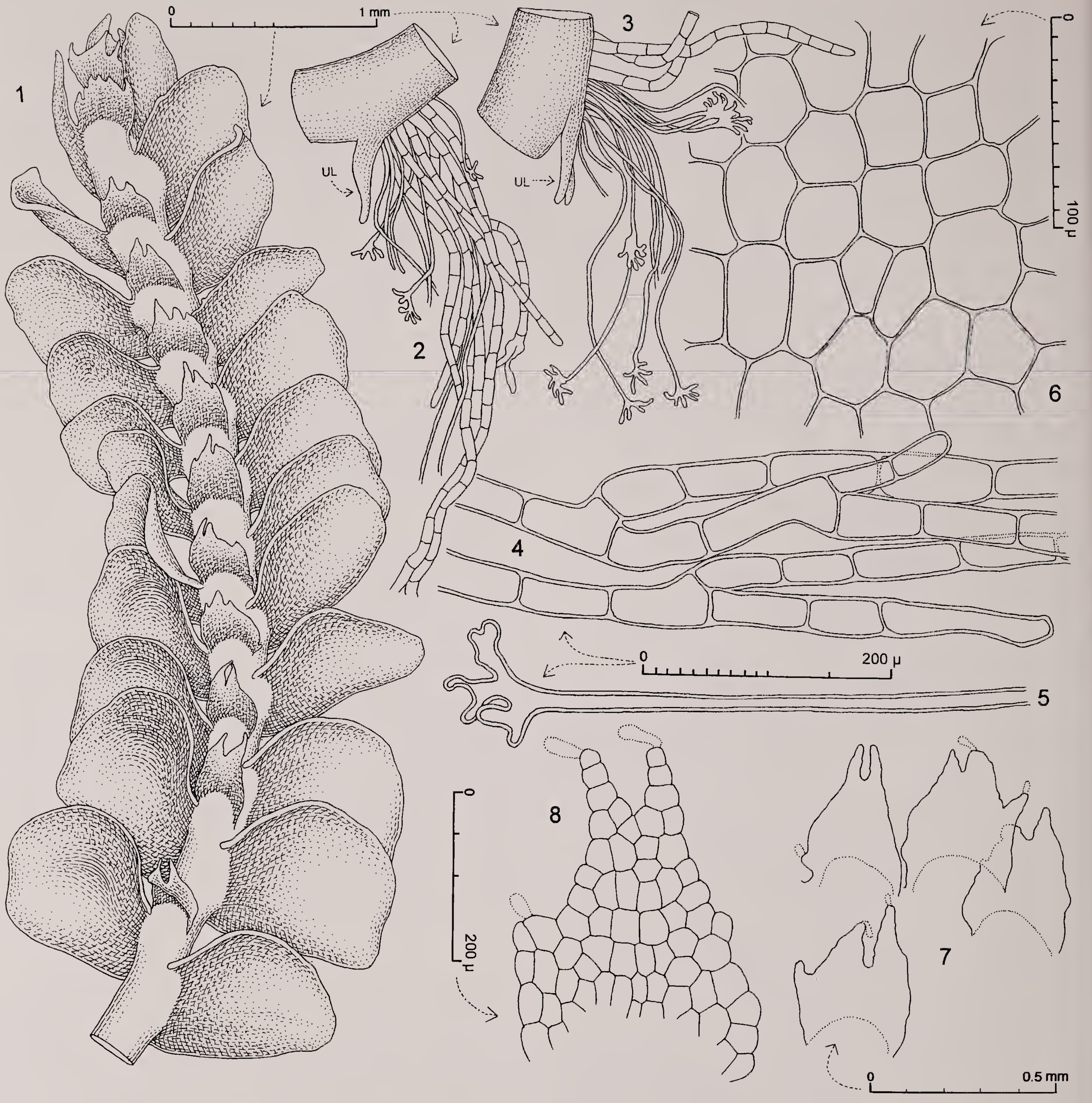

FIG. 46. *Chiloscyphus septatus* J. J. Engel. **1.** Portion of leading shoot, ventral view. **2, 3.** Shoot sectors, lateral view, showing septate and nonseptate rhizoids (ul = underleaf). **4.** Septate rhizoids. **5.** Nonseptate rhizoid. **6.** Median leaf cells. **7.** Four underleaves. **8.** Underleaf. (All from type.)

branched (Fig. 46: 2, 3, 5). Rhizoids of this type, however, do not branch below the tips, as is typically the case in most leafy Hepaticae. Other rhizoids are wider (26–36 μm wide), regularly septate and never have peg-like swellings of the interior wall (Fig. 46: 2–4). The septate rhizoids occasionally branch, but the branches occur below and never at the tips (Fig. 46: 4). The septate rhizoids may be present with nonseptate ones in a fascicle at the underleaf base (Fig. 46: 2, 3) or may be some distance removed from the underleaf base and then ± scattered. Septate rhizoids are exceptional in leafy Hepaticae. They are present, for example, in *Telaranea monocera* Mitt. ex J. J. Engel & G. L. Merr. (Engel and Merrill, 2004). That species may have asymmetric underleaves (Schuster, 2000, figs. 194: 4; 195: 1), with the shorter lobe consisting of a single cell plus a slime papilla, and an elongate, septate rhizoid appears to originate from the basal cell. Septate rhizoids also occur throughout *Pachyschistochila* R. M. Schust. & Engel (Schuster and Engel, 1985). The septate

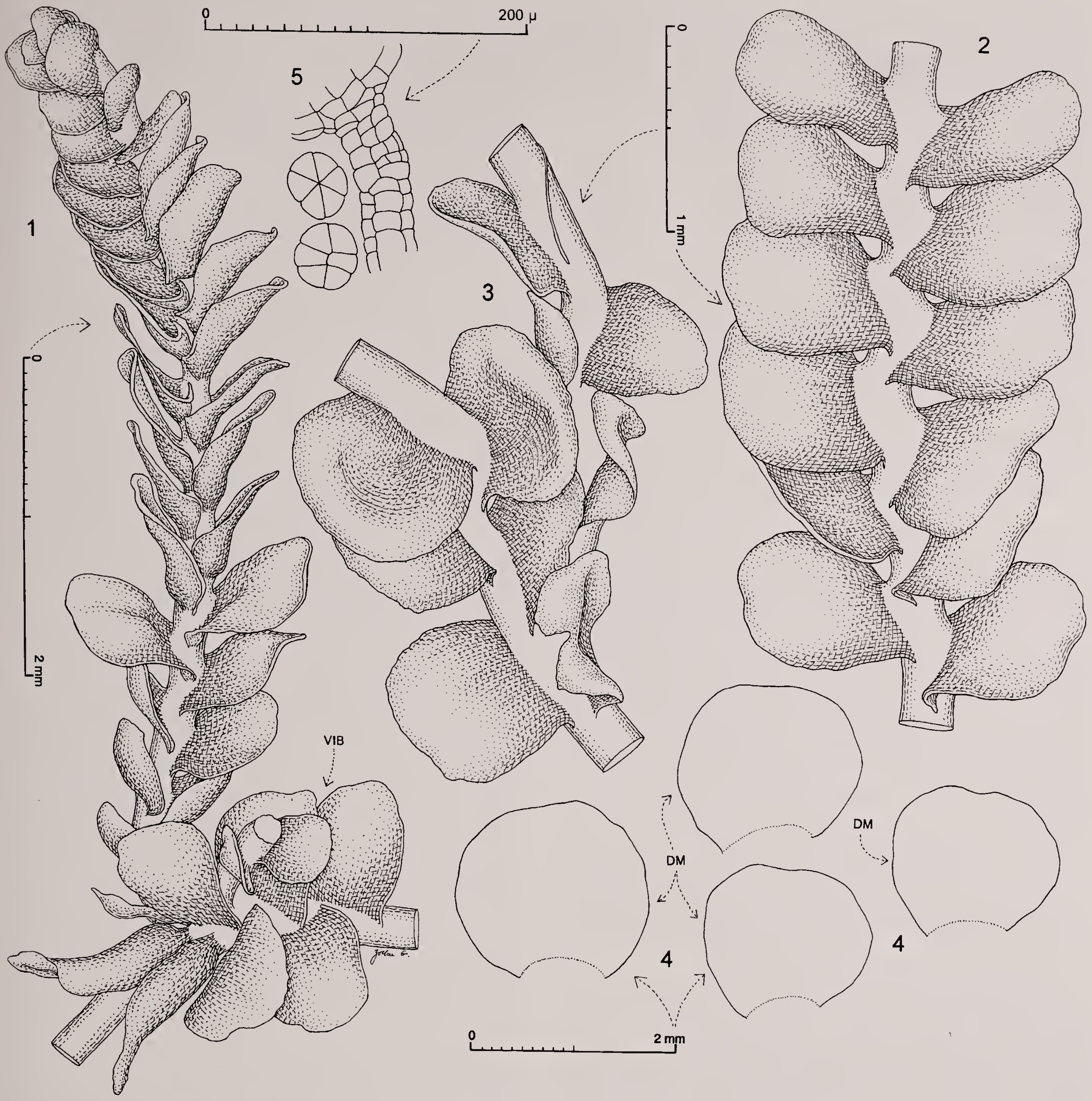

FIG. 47. *Chiloscyphus septatus* J. J. Engel. **1.** Portion of main shoot with androecium, a short ventral-intercalary branch (= vib) and a ventral-intercalary branch with a pair of ♂ bracts basal in position on the branch; dorsal view. **2.** Portion of main shoot, dorsal view. **3.** Portion of main shoot with *Frullania-type* branch (= FB; hl = half-leaf); dorsal view. **4.** Four leaves (dm = dorsal margin). **5.** Antheridial stalk, and to left, 2 cross sections. (All from type.)

rhizoids of *C. septatus* are not associated with asexual reproduction (see Schuster, 1966, p. 511).

DISTRIBUTION AND ECOLOGY—Known only from the type, which occurred on soil over a boulder of a stream bed (subject to inundation) in a steep-sided valley bottom within a forest of *Beilschmiedia*, *Vitex*, *Hoheria*, and *Cyathea dealbata*.

Chiloscyphus* subg. *Connati (Lindenb.) J. J. Engel

Plagiochila sect. V. *Connatae* Lindenb., Spec. Hep. XXIX. 1839. *Lophocolea* subg. *Connatae* (Lindenb.) Piippo, Ann. Bot. Fenn. 131: 165. 1985. *Chiloscyphus* subg. *Connati* (Lindenb.) J. J. Engel, Novon 9: 22. 1999. Type (cf. Piippo, 1985, p. 165): *Chiloscyphus ciliolatus* (Nees) Gottsche.

Leaves subopposite to opposite, consistently and often asymmetrically bilobed, the ventral lobe frequently larger than the dorsal. Trigones consistently knot-like (exc. *C. spinifer*), but with thin intervening walls. Underleaves large, conspicuous, broad, concave (exc. *C. spinifer*), distinctly and at times broadly connate on both sides. Antheridial stalks biseriate. Gynoecium with bracteoles large, often broadly connate on both sides, concave, rarely plane; vestigial perigynium present, at least the innermost whorl of bracts and bracteole inserted on it. Innermost capsule wall cells with tangential semiannular bands often furcate and anastomosing to delimit fenestrae.

The subgenus is described by Piippo (1985) for the "*Lophocolea ciliolata*" group, and is comprised of a suite of paleotropical-Oceania species. This concept of the subgenus corresponds to my circumscription of sect. *Connati.* I have expanded the perimeters of the subgenus to include the monotypic sect. *Spiniferi*, a group of Australasian tuberculate taxa, the *Leucophylli*, and sect. *Connati.*

Section *Bicornutae* (Spruce) J. J. Engel & R. M. Schust. (Engel and Schuster, 1985, p. 409) belongs here, and is an ally to sect. *Connati.* The *Bicornutae* differ from the *Connati* in being leptodermous (see comments on sect. *Bicornutae* in Schuster, 1980).

The subgenus is pan-tropical and temperate Australasian in range.

Sect. *Spiniferi* J. J. Engel

Chiloscyphus sect. *Spiniferi* J. J. Engel, Novon 9: 22. 1999. Type: *Jungermannia spinifera* Hook. f. & Taylor

Leaf apices subequally bilobed. Leaf, underleaf, and perianth cells smooth, without protuberances. Leaf cells with small trigones. Underleaves exceedingly large, asteroid, (4)6-lobed, narrowly connate on both sides. Plants dioecious.

This monotypic section, restricted to New Zealand, occupies an isolated position in subgenus *Connati* in having small trigones and exceptionally large, (4)6-lobed underleaves. Yet the presence of biseriate antheridial stalks, fenestrate inner capsule wall cells, subopposite leaves, and underleaves connate on both sides dictate placement in that subgenus. The section is allied to the *Leucophylli.*

Chiloscyphus spinifer (Hook. f. & Taylor) J. J. Engel & R. M. Schust.

Jungermannia spinifera Hook. f. & Taylor, London J. Bot. 3: 381. 1844. *Lophocolea spinifera* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 163. 1845. *Chiloscyphus spinifer* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 423. 1985 (1984). Lectotype (*nov.*) Auckland Is., Nov. 1840, *Hooker* (FH!–c. ♂); isolectotypes: (BM [2]!–c. ♂) (all admixed with *Lepidozia* sp. and a Dicranaceous moss).

Plants subisophyllous, with a spiny appearance in ventral view, prostrate to ascending to erect, pale green to whitish green to light yellow green, rather translucent; shoots medium, to 3.4 mm wide. Branching copious, 1–2 (rarely 3) pinnate, the primary branches elongate and slender, the secondary and tertiary branches short, the main shoots frequently decaying; branches of *Frullania* and lateral-intercalary types, the former overall slightly prevalent. Stems rather narrow for plant size, 10–11 cells high, the cortex slightly differentiated, in 1–2 layers of slightly thick-walled cells; medullary cells thin walled, largest in center of stem. Rhizoids from stem at immediate base of underleaves. Leaves with a delicate appearance, subopposite (but not clearly so because of very dense imbrication), the leaves horizontal, the basal portion strongly dorsally assurgent, but the distal portion decurved, the leaves widely spreading, free dorsally, orientation strongly succubous, the insertion long oblique, the lines of insertion extending to stem midline dorsally and thus without a leaf-free strip of stem cells, the leaf arrangement practically covering the stem in dorsal view except for a very narrow "zigzag" strip which is especially pronounced on branches. Leaves convex, especially so distally, asymmetrically deltoid, clearly widest near base, the apex rather narrow, well-developed leaves wider than long; apex bifid to 0.2–0.3, the lobes mostly parallel to slightly diverging, often sharply deflexed, plane to slightly ventrally sulcate at the base, subequal in size or the ventral a little larger, the lobes acuminate, the tip terminating in a uniseriate row of 3–5 cells, the lobe margins entire; dorsal margin much longer than the ventral, straight or with a line slightly arched toward the base and curved slightly inward distally, entire, abruptly and sharply deflexed, and forming a cnemis which is ill-defined distally but distinct at the margin base, the dorsal margin short decurrent; ventral margin slightly to broadly rounded but with a short constriction near the base, plane to slightly deflexed, entire or with 1–3 or more narrow laciniae. Leaf cells decidedly biconvex, the swellings thin walled, particularly evident in leaf profile, the cells dimorphic: most cells thin walled and with small, concave-sided trigones, but scattered among them are cells with walls secondarily thickened; median leaf cells 23–33(–36) µm wide, 30–43 µm long; surface smooth. Oil-bodies in all leaf cells except distalmost 1–2 cells of leaf lobes, occupying fraction of cell volume, hyaline, ± glistening, 2–4 to 3–6 per cell, finely papillose or rather coarsely botryoidal, narrowly to less often broadly elliptic to fusiform, often bacilliform, sporadically with an indentation or furrow, sporadically globose, 6.5–7.8 × 2.6–3.3 µm, sporadically 9.1 × 3.3 µm, globose ones 3.3–3.9 µm in diam. Underleaves exceedingly large for plant size, the width (including lateral lobes) 1.2–1.9× the leaf length, the underleaves (*in situ*) on each side extending laterally as far as leaf tips or nearly so, the underleaves narrowly connate on both sides, the insertion symmetric or nearly so, inverted U-shaped, the underleaves moderately spreading to squarrous to broadly reflexed and then with a major portion of the adaxial surface of the underleaf visible in ventral view; underleaves imbricate, closely so on branches, broadly convex (ventral view), much wider than long (width includes lateral lobes), palmately 6-lobed (4-lobed in weaker plants), the lobes of ± equal size, the median sinus divided to 0.4–0.7 by a broadly rounded to lunate sinus; lobes diverging laterally, often strongly so, long apiculate to acuminate from a broad base; median and lateral lobes often ventrally sulcate, mostly entire, occasionally with 1 or 2 large teeth or laciniae toward base; lamina margins entire or with a few teeth near base, not to long decurrent before connation with leaves.

Asexual reproduction absent.

Plants dioecious. Androecia subfolious, on main shoots and elongate *Frullania*-type branches, initially terminal but becoming intercalary. Bracts subfoliaceous, similar to leaves in shape, form, and imbrication, except the bracts are a little more dorsally assurgent, are slightly to moderately smaller, and have a dorsal pocket, the bracts free dorsally but the saccate portion fused toward base with opposite bract, the bracts rather locally ventricose in dorsal-basal portion; lobule small for bract size, the margin involute to form a pouch, crenate, with a few projections of 2 superposed cells, otherwise crowded with numerous slime papillae; antheridia solitary, the stalk rather short, 12–13 cells long, biseriate. Gynoecia on main shoots and moderately long *Frullania*-type branches; subfloral innovations absent; vestigial stem perigynium present, fleshy, 7–9 cells thick near level of foot–seta juncture, with 3–4 pairs of bracts and bracteoles inserted on the vestigial

TABLE 11. Comparison of phenotypic extremes of *Chiloscyphus spinifer.*

Character	Mod. *planiamphigastria-entirefolia*	Mod. *reflexiamphigastria-lacinifolia*	Figure no.
Lateral-intercalary branch frequency	common	rare or sporadic	
Underleaf juxtaposition with stem	spreading but not reflexed	often broadly reflexed	48: 5
Depth of median sinus of underleaf	0.6–0.7	0.4–0.6	48: 11 50: 4
Underleaf connation	long decurrent prior to connation with leaves, the underleaf thereby apical to the leaves with which it is connate, the lateral base of the underleaf and the ventral margin of the attached leaf separated by gap	not decurrent prior to connation with leaves, the underleaf thereby closely juxtaposed to and partially covering the leaves with which it is connate	48: 9 50: 5
Ventral margin of leaves	entire	often with 1–3 or more laciniae	48: 5 50: 5
Relative vigor	moderately developed plants, shoots 1.8–2.2 mm wide	vigorous, often robust plants, shoots 2.6–3.4 mm wide	
Habit	prostrate to slightly ascending	suberect to erect	
Ecology	pioneer on wood usually sparsely covered by other bryophytes, less often on shrub branches	bryophyte covered, often very rotted logs, less often on soil or bryophyte-covered boulders	

stem perigynium. Bracts of innermost series much larger than leaves, usually erect and ensheathing perianth but occasionally obliquely spreading from an appressed base, free from one another, strongly convex to subcanaliculate, ± asymmetrically elliptic (the dorsal margin more strongly arched than the ventral); apices bifid to ca. 0.2 by acuminate lobes, the lobe margins ventrally sulcate, entire; lamina margins strongly reflexed, with several laciniae. Bracteoles of innermost series somewhat smaller than bracts, narrowly connate on both sides, distinctly concave (ventral view), subcuneate; apices truncate, 4-lobed to ca. 0.3, the apex with a few accessory laciniae; lamina margins with a few laciniae distally and sparingly dentate toward the base. Perianth barely to distinctly exserted beyond bracts, sharply trigonous throughout, with 1 of lateral sides infolded nearly throughout, the perianths narrowly oblong to narrowly obovate, the mouth distinctly 3-lobed; lobes deeply bifid, the segments narrowly acuminate, entire, the lobes with several accessory sharp laciniae below the level of the segments; keelar wings common, of several cells high, with a few small laciniae.

Seta 10–11 cells in diam., with 36 rows of outer cells surrounding an inner core of scattered cells, the cells of the outer row ± similar to the cells immediately within, but the inner cells gradually increasing in size toward the center. Capsule rather short elliptic, 980–1120 µm × 630–840 µm, the wall 41–50 µm thick, of 5 layers, the outer layer of cells equal to thickness of 2.4–2.5 of interior strata; outer layer of cells subquadrate to short subrectangular, the radial walls thin, with red-brown nodular to weakly spur-like thickenings that are mostly on longitudinal walls and to a lesser extent on transverse walls, the longitudinal walls and transverse walls sporadically devoid of thickenings, the exposed tangential wall thickened; intermediate layers gradually diminishing in thickness toward innermost layer, which is thinnest, the intermediate layers with vertical thickenings often considerably tangentially extended, sometimes becoming semiannular; innermost layer of cells irregularly long rectangular, the radial walls with moderately thick continuous sheets of red-brown wall material, with semiannular bands red brown, abundant, narrow, the bands often nonpigmented (especially in median portion where at times faint), sometimes incomplete, often forked, often anastomosing to delimit ill-defined fenestrae, the radial walls without nodular thickenings, the exposed tangential wall very thin.

Spores 11.5–12.4 µm, pale brown, thin, minutely and finely punctate, the punctae not crowded, sporadically and locally coalescing but the markings remaining short, not vermiform; spore:elater diameter ratio 1.3–1.6:1. Elaters tortuous, 7.7–9.1 µm wide, the spirals 2.4–2.9 µm wide, loosely wound.

DIFFERENTIATION—*Chiloscyphus spinifer* is a well-defined species and is not likely to be confused with any other. It is one of a relatively few number of species recognizable even when dry, having in dorsal view a "channeled" appearance that was noted in the protologue. The condition is due to the close imbrication of leaves, resulting in only a very narrow "zigzag" strip of exposed stem. Moistened plants reveal the remarkably huge underleaves, being as wide as the shoot or nearly so, wider than the leaf length and with a remarkable similarity to leaves of the Plane tree (*Platanus*; Fig. 48: 5, 9).

Section *Spiniferi* is allied to the *Leucophylli. Chiloscyphus spinifer* may be initially confused with *C. mittenianus*, which is of similar size, has very large reflexed underleaves and deeply bifid leaves. I have studied several collections that involve misdeterminations of the two species. The smooth cells and deeply 4–6-fid underleaves will immediately distinguish *C. spinifer.*

VARIATION—The species is rather uniform in characters discernable in dorsal view. However, certain phenotypes may appear quite different from one another in features observed in ventral view. Much of the variability seems to be dependent on vigor, and a broad continuum connects the extremes. Table 11 contrasts the extremes.

Some populations have terminal and intercalary branching in about equal frequency (mod. *planiamphigastria-entirefolia*). Plants of mod. *reflexiamphigastria-lacinifolia*, however, have *Frullania*-type branches prevalent, with intercalary branching grading from frequent to sporadic to rare.

NOTES—1) The underleaf width was measured by extending a line between opposing tips of lateral lobes (Fig. 1: 3). Measurements were done in this fashion because the underleaf lamina has little definition due to the exceedingly large lateral lobes.

2) Underleaf connation is narrow (Fig. 48: 5, 9) and best observed by rotating the shoot in both directions to obtain ventral-lateral views of leaf–underleaf attachment.

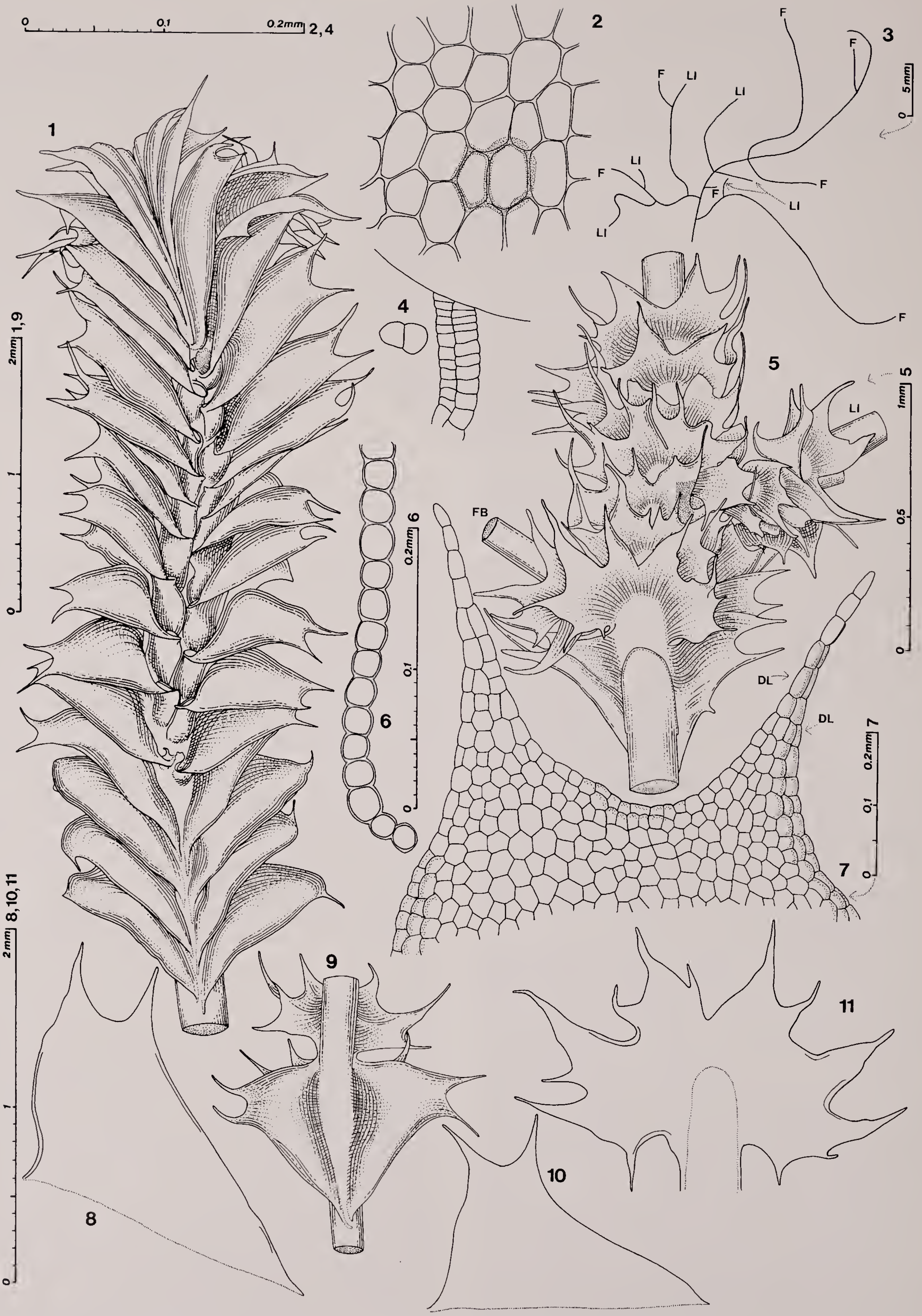

FIG. 48. *Chiloscyphus spinifer* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. (**8–11,** from *mod. planiamphigastria-entirefolia*). **1.** Androecium-bearing shoot. **2.** Median leaf cells. **3.** Cladograph (F = *Frullania*-type branch; LI = lateral-intercalary branch). **4.** Antheridial stalk and, to left, stalk cross section. **5.** Portion of shoot with, at left, *Frullania*-type branch and, at right, lateral-intercalary branch; the collar seen in profile (ventral view). **6.** Leaf, cross section. **7.** Distal portion of leaf (dl = dorsal lobe). **8, 10,** Leaves. **9.** Leaf pair and underleaf. **11.** Underleaf. (**1, 4,** from *Engel 17855*, New Zealand, South Is., SW of Mt. Brewster; **2, 3, 5–11,** from *Engel 17849*, same loc.)

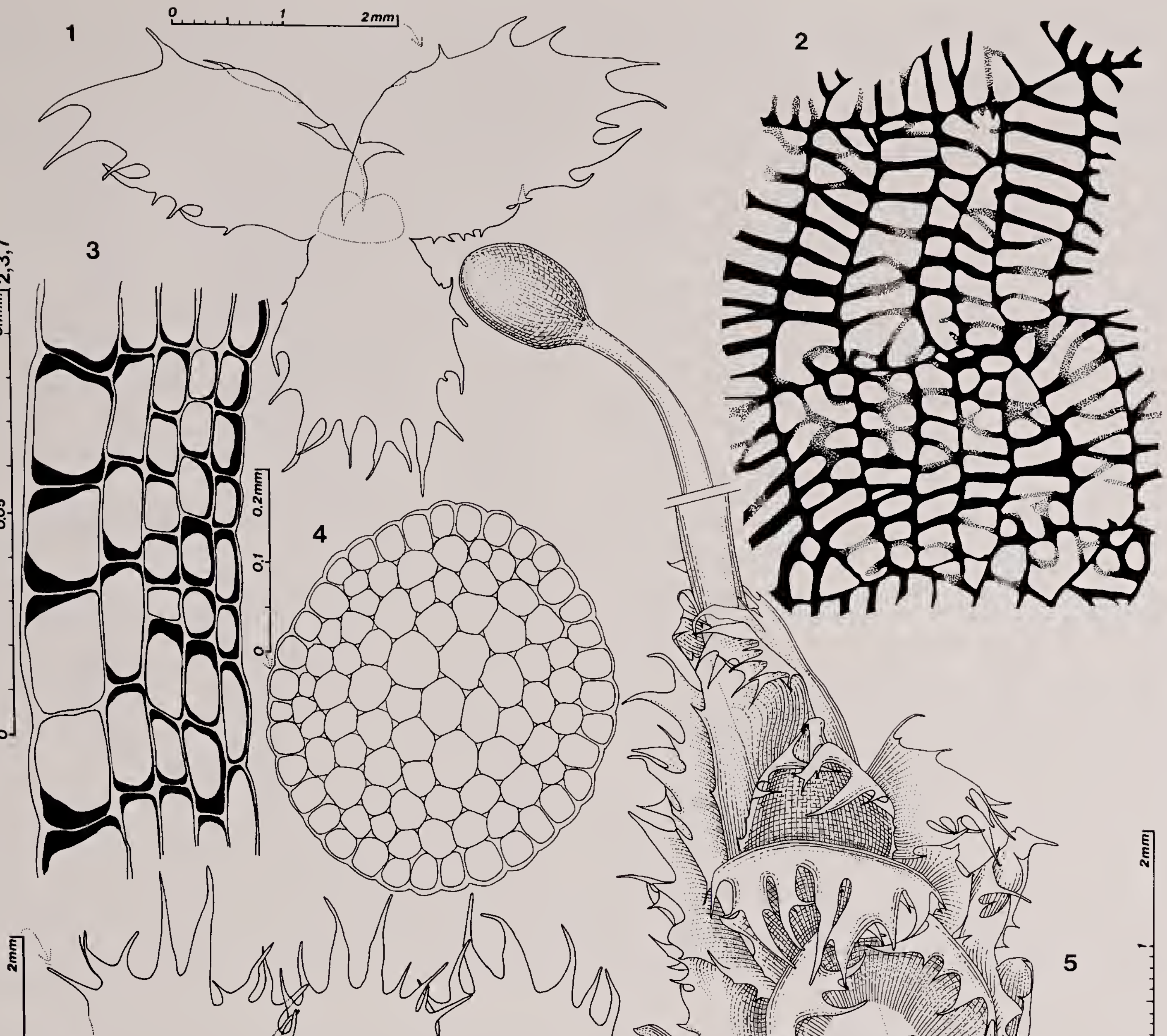

FIG. 49. *Chiloscyphus spinifer* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **1.** ♀ Bracts and (below) bracteole (note, figure drawn a 0.5× the scale of leaves and underleaves). **2.** Capsule wall, inner layer. **3.** Capsule wall, cross section. **4.** Seta, cross section. **5.** Gynoecium with mature sporophyte, ventral view; the level of sporophyte foot indicated with stipple. **6.** Perianth mouth, ventral lobe in middle. **7.** Capsule wall, outer layer. **8.** Vestigial stem perigynium, cross section just distal to foot–seta juncture (br = bracts). (All figures from *Engel 17855*, New Zealand, South Is., SW of Mt. Brewster.)

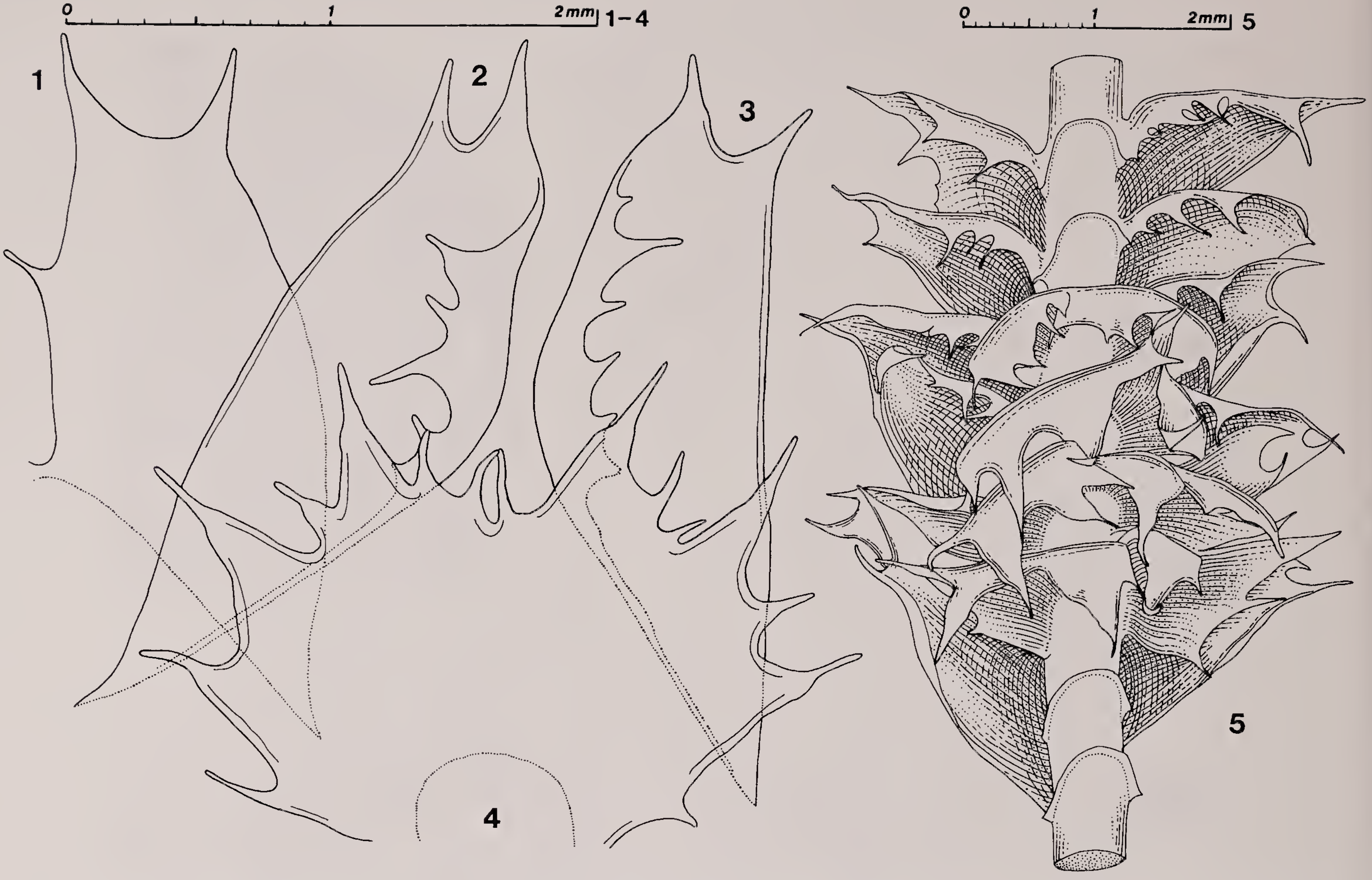

Fig. 50. *Chiloscyphus spinifer* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. (mod. *reflexiamphigastria-lacinifolia*). **1–3.** Leaves. **4.** Underleaf. **5.** Portion of axis, ventral view. (**1–3, 5,** from *Engel 17855*, New Zealand, South Is., SW of Brewster; **4,** from *Engel 18840*, New Zealand, South Is., Tutoko River.)

Distribution and Ecology—Endemic to New Zealand. The species occurs on Auckland Is. and is restricted to the western sector of South Is. ([50–]305–1380 m) and to sporadic stations at upper elevations of North Is. (670–1320 m); also on Rangiawia (Pitt I.). The species is rather common in wet, rich *Nothofagus* (particularly *N. menziesii*) and mixed *Podocarpus* forests where it occurs on old logs, particularly bryophyte-covered, rotted wood on the forest floor and tree bases, and in these situations it may form extensive, often pure, thick mats. It occurs to a lesser extent on the forest floor or on boulders of stream banks. The species also occurs in ecotonal areas between forests of either *N. menziesii* or *N. solandri* var. *cliffortoides* and the subalpine zone and extends into subalpine areas of snow tussock, *Dracophyllum*, *Olearia*, *Celmisia*, *Empodisma minor*, and others. At the summit area of Te Rangaakapua (Urewera Natl. Park, 1265–1320 m), it forms soft pure colonies on trunks of *Olearia* in mosaics of stunted *Olearia colensoi* and tussock (*Engel 23429*).

Specimens Seen (selected)—**AUCKLAND IS.:** Waterfall Inlet, sea level, *Dawbin s.n.* as *L. leucophylla*–c. per. (CHR). **NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, 11.3 km by road WNW of Borland Lodge, above South Branch of Borland Burn, W of Monowai, 680 m, *Engel 18733* (F); ibid., off track to Island Lake, just W of Borland Saddle, S of South Branch of Borland Burn, W of Monowai, 800 m, *Engel 18627*–c. sporo. (F); ibid., Dusky Sound, Supper Cove, *Simpson 3765* as *L. leucophylla* (CHR); ibid., Fiordland Sound Track, near Wilmot Pass, Doubtful Sound Track, between midway hut (E of pass) and pass itself, 490–640 m, *Schuster 52709* (F); ibid., Doubtful Sound, Snug Cove, *Allan s.n.* (CHR); ibid., Secretary Is., *Taylor & Party s.n.* (CHR); ibid., Cascade Creek, near Lake Gunn, tributary of Eglinton River, ca. 365 m, *Child H 2602*–c. ♂ (F); ibid., Central Earl Mtns., Mistake Creek, between Triangle Peak and Melita Peak, NE of northern end of Lake Te Anau, 740–800 m, *Engel 18783* (F); ibid., Lake Gunn, *Zotov s.n.* (CHR); ibid., Lake Marion Track, on Hollyford River, at foot of Mt. Christina, *Schuster 55704* (F); ibid., S end of Lake Marion, W of Hollyford River, 695 m, *Engel 23171* (F); ibid., Lake Marian Valley, ca. 305 m, *Child H 2945* (F); ibid., Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel 23215* (F); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18840* (F). **OTAGO:** Route Burn Valley, ca. 520 m, *Child H s.n.120* (F); Route Burn Mtns., *Zotov s.n.* (CHR); Beans Burn, tributary of Dart River, 455 m, *Child 1294*–c. sporo. (F); Fiordland Natl. Park, Humboldt Mtns., above Lake Mackenzie, *Schuster 67-267*–c. ♂ (F); ibid., ibid., N of Earland Falls, on track to Lake Mackenzie, *Schuster 67-3454A*–c. ♂ (F); ibid., trail between Hidden Falls and Gunn's Camp, SE of Martin's Bay, *Hatcher 1499* (F); ibid., head of Lake McKerrow, *Hatcher 723* (F); ibid., ibid., near McKerrow hut, *Hatcher 1737* (F); Mt. Aspiring Natl. Park, Blue River near confluence with Makarora River, NNE of Makarora, 310 m, *Engel 18910*–c. ♂ (F); ibid., Makarora River, near base of Haast Pass, *Allison H 5976* as *L. leucophylla* (CHR); opposite Siberia Hut, tributary of Siberia Stream, WNW of Makarora, ca. 760 m, *Child H 2980* (F). **OTAGO/WESTLAND PROV. BOUNDARY:** Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel 18014*–c. sporo. + ♂; Haast Pass, ca. 610 m, *Child H 4510* (F); Mt. Brewster, ca. 1065 m, *Child H 4204* (F). WESTLAND: Mt. Aspiring Natl. Park, off track to Mt. Brewster, below and W of Mt. Armstrong, SW of Mt. Brewster, ca. 900 m, *Engel 17855*–c. sporo. + ♂ (F); ibid., Cross Creek, 1 km N of Haast Pass, 510 m, *Engel 21872* (F); Fox Glacier, on trail to Cone Rock, *Schuster 67-3214* (F); Westland Natl. Park, Franz Josef Glacier Valley, off Roberts Point Track, SW of Mt. Gunn, ca. 510–570 m, *Engel 18132* (F); ibid., track to Alex Knob just below juncture with track to Louisa Peak, 1150–

1170 m, *Engel 18996* (F); Kelly Range, *Beckett s.n.* (M); Arthur's Pass Natl. Park, N of Kelly Creek near Hwy 73, above campground, N of Otira, 420–475 m, *Engel 18354* (F); Camp Creek, W of Alexander Range, 530–880 m, *Reif C102B* (F); Paparoa Range, ridge immediately N of Sewell Peak, 890–910 m, *Engel 19020*–c. per. (F); ibid., cirque on E flank of Mt. Priestly, W bank of tarn, 960 m, *Fife 5570* as *L. leucophylla* (F), *5561* (NY); ibid., N flank of Mt. Euclid, ca. 0.5 km SE of Morgan Tarn, *Fife 6459* (F); same loc., 1100 m, *Beever s.n.* as *L. aculeata* (AK). **CANTERBURY:** Upper Poulter River Valley, *D. Scott s.n.* as *L. leucophylla* (CHR); Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel 18470*–c. ♂ + per. (F); ibid., near Bealey Glacier Vista, *Engel 6851*–c. per. (F); ibid., Bealey Track (to Bealey Glacier), within 1.5 km NW of Jack's Hut, *Fife 6146, 6148*, both as *L. leucophylla* (F). **NELSON/CANTERBURY PROV. BOUNDARY:** Cannibal Gorge, Lewis Pass, ca. 610 m, *Child H 4622* (F). **NELSON:** Garibaldi Ridge, immediate vicinity and at peak of Gordon's Pyramid, ca. 1280–1380 m, *Engel and von Konrat 27138* (F); Mt. Augustus, NE of Westport, 700 m, *Dugdale s.n.* (CHR, F); Mt. Arthur, Tableland Track, *Sainsbury s.n.* as *L. decurrens* (CHR); near Salisbury Lodge, ca. 1100 m, *Brown 88/85b* (AK); Mt. Arthur, Mt. Arthur Hut Track, 1050 m, *Engel 24923* (F); Abel Tasman Natl. Park, Mt. Evans, ca. 1065 m, *Child H 4706* (F). **MARLBOROUGH:** Mt. Robertson, SSE of Picton, ca. 915 m, *Child H 4395* as *L. leucophylla* (F). **NORTH ISLAND. WELLINGTON:** Akatarawa, Waiotauru Road, ca. 670 m, *Braggins 84/394* as *L. leucophylla* (AK); Tararua Range, Mt. Holdsworth, 795 m, *Butler 2538* (CHR); Central Ruahine Mtns., Hikurangi Range, *H. Hodgson s.n.*–c. per. + ♂ (CHR); NW Ruahine Mtns., "Otupae," *Druce s.n.* (CHR); Tongariro Natl. Park, ca. 8 km from Ohakune on Ohakune Mtn. Road, ca. 950 m, *Engel 21337*–c. per. (F). **GISBORNE:** Lake Waikare-iti, Waikaremoana, 915 m, *Hodgson 613* (CHR); Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20589* (F); ibid., Huiarau Range, summit area of Te Rangaakapua, 1265–1320 m, *Engel 23429* (F). **NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY:** Urewera Natl. Park, track to Whakataka Hut from Lake Waikaremoana, N of western extremity of Lake Waikaremoana, 1000–1100 m, *Engel 23310*–c. per. (F). **Rangiawia (Pitt I.):** Hakepa Hill, 220 m, *de Lande CH1989 & Heenan* (AK, F).

Chiloscyphus **sect.** ***Connati*** (Lindenb.) J. J. Engel, **comb. nov.**

> *Plagiochila* sect. V. *Connatae* Lindenb., Spec. Hep. XXIX. 1839. Type: *Chiloscyphus ciliolatus* (Nees) Gottsche.

Branching commonly to exclusively lateral-intercalary, sometimes also terminal-lateral, the ventral-intercalary type absent. Leaves short bilobed, mostly asymmetrically so, the ventral lobe larger than the dorsal. Leaf, underleaf, and perianth cells smooth, without protuberances. Underleaves very broadly connate on both sides, 2–4-lobed, without conspicuous basal teeth. Perianth with keelar wings common (exc. *C. helmsianus*), exceptionally high, often armed. Plants dioecious, autoecious or paroecious.

The "*Lophocolea ciliolata*" group, outlined in Piippo (1985), have a range that includes tropical Asia, with disjunct representatives in New Caledonia and Hawaii. Apparently also belonging here are:

> ***Chiloscyphus ceylonensis*** J. J. Engel, ***nom. nov.*** *pro Lophocolea fleischeri* Steph., Spec. Hep. 3: 132. 1906 *non Chiloscyphus fleischeri* Steph., Spec. Hep. 6: 306. 1922. Type: Ceylon, *Fleischer.*
> ***Chiloscyphus regularis*** Steph., Hedwigia 32: 325. 1893. Type: Réunion, St. Pala, Rivière de Roches, *Lepervanche.*
> = ***Lophocolea onraedtii*** Grolle, J. Hattori Bot. Lab. 55: 505, *f. 1.* 1984. Holotype: Réunion, Greande-Montée, Col de Bellevue, 1850 m, *Onraedt 73.R.4325* (hb. Onraedt, *non vidi*).

The species occurs in Réunion and Madagascar (see Grolle, 1984).

Taxa treated herein extend the range of the section into temperate Australasia.

Key to Australasian Taxa of Sect. *Connati*

1. Underleaves divided to at most 0.5; androecia chiloscyphoid, i.e., subfoliose, on main shoot or lateral-intercalary branches that often considerably exceed the length of the leaf immediately above and that have vegetative leaves. Plants dioecious 2

    2. Ventral lobe of leaf various, grading from acute to acuminate, sometimes apiculate, terminating in a uniseriate row of 1–4 at most slightly elongated cells; dorsal and ventral margins of leaf entire, the ventral margin rarely with a tooth. Tasmania 3

        3. Branching nearly exclusively lateral-intercalary; leaf apices asymmetrically short bifid: the dorsal lobe much smaller and often reduced to a small tooth or rounded projection; leaves horizontal and widely spreading, the orientation strongly succubous; leaves often connate dorsally; plants larger, to 5 mm wide; oil-bodies 3–5 per cell. Plants of forests . . . . *C. suboppositus* (p. 143)

        3. Branching predominantly to exclusively of *Frullania* type; leaf apices variable: narrowly rounded to retuse-bidentate to symmetrically or asymmetrically short bifid to 1-dentate; leaves vertical to subvertical, strongly dorsally assurgent and mostly erect to suberect, the orientation subtransverse to subsuccubous; leaves consistently free dorsally; plants smaller, to 2.2 mm wide; oil-bodies 2(3) per cell. Plants subalpine/alpine and in higher elevation forests . . . . *C. edentatus* (p. 152)

    2. Ventral lobe of leaf subcaudate to piliferous, terminating in a uniseriate row of 5–7(8) elongated cells; dorsal and ventral margins of leaf each often with 1–3 ciliiform processes. Leaves bifid to 0.2–0.25, the dorsal lobe only sporadically basal in juxtaposition to the ventral lobe. New Zealand . . . . [*C. aculeatus* p. 161]

1. Underleaves divided to 0.5–0.8; androecia at least at times heteroscyphoid, i.e., spicate and restricted to abbreviated, lateral-intercalary branches that do not exceed the length of the leaf immediately above, the branches at least with a few vegetative leaves 4

    4. Vegetative and sexual branches strictly lateral-intercalary; plants dioecious; perianth barely exserted beyond bracts, short obovate to short oblong. New Zealand 5

        5. Underleaves asymmetrically connate: broad on 1 side, narrower, longer and more basal on the other; leaves often connate dorsally, the lobes with a uniseriate row of 4–9 cells; branch origin highly variable, not restricted to any position; median leaf cells 20–30 µm wide × 26–36 µm long; plants, especially when fresh, with a strong odor . . . *C. helmsianus* (p. 134)

        5. Underleaves symmetrically connate: the two sides ± equally broad, the connation length on each side ± equal; leaves free dorsally, the lobes with a uniseriate row of 2–4 cells; branch origin consistently immediately dorsal to leaf–underleaf connation; median leaf cells 30–36 µm wide × 36–49 µm long; plants lacking a noticeable odor . . . . *C. multipennus* (p. 137)

4. Vegetative and androecial branches often of *Frullania* type (sporadic exceptional populations aside); plants autoecious; perianth longly exserted beyond bracts, 5–6× longer than wide. Underleaf margin defining the median sinus sometimes 1–2-dentate-laciniate; plants pale-translucent. New Zealand, Tasmania, Australia (NSW) ..... *C. trialatus* (p. 147)

Chiloscyphus helmsianus (Steph.) J. J. Engel & R. M. Schust.

> *Lophocolea helmsiana* Steph., Bull. Herb. Boissier 6(9): 794. 1906 (= Spec. Hep. 3: 94). *Chiloscyphus helmsianus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 416. 1985 (1984). Type: New Zealand, South Is., without specific loc., *Helms s.n.* (G!–c. sporo.).

Plants very fragile, translucent, rather stiff, dorsiventrally flattened, with a superficial plagiochiloid appearance (especially when dry), prostrate, light olive green in herb., highly nitid when dry; shoots to 3.1 mm wide, strongly scented, especially when fresh. Branches very common, all of lateral-intercalary type, the position variable: lateral and then immediately above leaf–underleaf connation, to ventral-lateral, and then between ventral leaf bases or between underleaf bases or in lateral half of underleaf axil, varying to ventral and then between 2 underleaves (but never in an underleaf axil). Stems narrow for plant size, 8–9 cells high, the cortex poorly differentiated, in 1 (locally 2) layers of cells somewhat smaller than those of the medulla, the walls of both cortical and medullary cells thin, or cortical cell walls faintly thickened. Rhizoids sparsely developed, where present few and from stem at base of underleaf. Leaves rigid, subopposite, horizontal, widely spreading, approximate, only the dorsal-basal sector overlapping the leaf immediately below, free or (often) connate dorsally, the orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves plane to feebly convex, subsymmetrically rather narrowly ovate to narrowly subdeltoid, occasionally subrectangular, the dorsal-basal sector dilated and acute, the extremity long decurrent, the leaves clearly widest near base; apex bifid to 0.15–0.25, the lobes mostly ± parallel to somewhat diverging, plane, subequal or, more often, the ventral larger, acuminate to subcaudate, frequently broken, especially on lower sector of shoots, the tip often piliform, consisting of a uniseriate row of 4–9 cells that are for the most part somewhat to distinctly longer than wide, the lobe margins entire; dorsal margin straight to broadly and gently curved, frequently broadly curved inward near base, plane to feebly deflexed, occasionally rather strongly and abruptly deflexed and then forming a weak cnemis, mostly entire, occasionally with a ciliiform process near lobe base; ventral margin straight to broadly and gently curved, plane, for the most part entire, but most shoots have at least some leaves with 1(2)-dentiform-ciliiform processes particularly near lobe base. Leaf cells with walls thin, trigones optimally knot-like (minute to medium in suboptimal populations), median leaf cells 20–30 µm wide, 26–36(43) µm long, thin walled and with bulging and knot-like trigones; surface smooth. Underleaves with median and distal cells of lamina lacking trigones. Underleaves much smaller than leaves, 1.1–2.3× stem width, connate on both sides: distinctly so on 1 side and ± narrowly so and somewhat more basal (often by the strip of decurrent underleaf tissue) on the other, the insertion often asymmetric, inverted U-shaped, with 1 side longer than the other, the lamina distant from one another but the lobe tips at times overlapping base of underleaf immediately above, the underleaves concave (ventral view), narrowly ovate-subrectangular grading to cuneate, bifid to 0.65–0.8, the lamina often only 4–7 cells high; lobes seldom complete, at least in part broken, ± parallel to strongly diverging, subcaudate-caudate, the distal portion consisting of a uniseriate row of 4–7 cells, the lobe margins usually entire, occasionally with a ciliiform-laciniiform process on margin defining sinus; lamina margins slightly recurved, entire or on each side with a process grading from ciliiform to laciniiform.

Asexual reproduction possibly by fragmenting leaf tips, otherwise absent.

Plants dioecious. Androecia on main shoots or lateral-intercalary branches issuing from median and basal sectors of main shoot, the branch position similar to sterile branching vis-à-vis lateral-ventral variability; androecia of basically 2 ± intergrading types, the extremes being: 1) short, determinate, heteroscyphoid, spicate, and not exceeding length of leaf immediately above and 2) indeterminate, chiloscyphoid, subfolious, and basal, terminal, or intercalary on elongate branches; androecia very rarely (1 branch seen) on a *Frullania*-type branch (then elongate and indeterminate). Bracts somewhat to much smaller than leaves, subvertical to vertical, strongly dorsally assurgent and inflated in basal half, the distal half either also stiffly assurgent and plane or ± reflexed and then weakly convex, the bracts loosely appressed to bract immediately above, the saccate portion ± crenulate in profile and fused toward base with opposite base; apex bilobed by acuminate to subcaudate lobes, the ventral lobe usually much larger than the dorsal, which is distinctly basal in juxtaposition to the ventral lobe; ventral margin entire or with 1(4)-dentiform-ciliiform processes; lobule margin involute, with a dentiform-laciniiform apical process and often 1 or 2 accessory teeth in sinus between apical tooth and base of dorsal margin of lobe, the free dorsal margin of lobule crenate but with several inflexed small teeth, cilia and copious simple and stalked slime papillae; antheridia solitary, the stalk biseriate; androecial paraphyses present, from base of inner or outer face of lobule near juncture with stem, the paraphyses pluricellular, irregularly ciliiform, simple or branched, irregularly armed, sometimes reduced and only 3 cells high. ♂ Bracteoles distinctly connate on both sides, differentiated from underleaves: ovate, less deeply divided, and more frequently entire margined. Gynoecia straight or slightly dorsally assurgent, on main shoot, or short to long lateral-intercalary branches, or (often) subfloral innovations. Bracts of innermost series much larger than leaves, erect or obliquely spreading (but appressed basally), free from one another or connate with each other, convex, narrowly ovate; apices deeply bifid, the ventral lobe larger than the dorsal, the lobe margins entire; dorsal margin plane or slightly reflexed, entire or 1–2-dentate-ciliate; ventral margin plane, 3–5-dentate-ciliate. Bracteoles of innermost series subequal to bracts in size or slightly smaller, connate on both sides but more narrowly so on one side, concave (ventral view), narrowly ovate; apices bifid to ca. 0.25–0.4, the lobes acuminate to sporadically subcaudate, the lobe margins entire or with a few teeth or cilia; lamina margins 1–4 ciliate-laciniate, often on each side with a prominent lacinium near lobe base. Perianth barely exserted beyond bracts, trigonous and prismatic throughout, short oblong to narrowly obovate, not to slightly expanding toward the wide, deeply 3-lobed mouth, the lobes free for ca. 0.4–0.5 the perianth length; lobes distinctly narrowed distally, deeply bifid, the segments caudate, entire, the lobes otherwise ciliate to laciniate below level of segments; keels sharp, with keelar wings occasional, when present low, short and not extending length of keel, rarely complete and armed.

Seta seen only in collapsed state. Capsule wall 34–36 μm, of 4 layers, the outer layer of cells equal to thickness of 1.9–2.5 of interior strata; outer layer of cells subquadrate to short rectangular, the radial walls with red-brown nodular to feebly spine-like thickenings mostly on longitudinal walls and sporadically on transverse walls; intermediate layers each thicker than inner layer, with vertical thickenings often considerably tangentially extended; innermost layer of cells irregularly rectangular, with semiannular bands red brown, common, narrow, usually complete, sporadically forked but never anastomosing to delimit fenestrae, the radial walls with nodular thickenings sporadic on both longitudinal and transverse walls.

Spores 10.1–11 μm, pale yellow brown, thin, with faint, low, close papillae and short vermiculate markings, spore:elater diameter ratio 1.1–1.3:1. Elaters tortuous, 8.2–9.6 μm wide, the spirals 1.9–2.4 μm wide.

DIFFERENTIATION—*Chiloscyphus helmsianus* is part of a suite of interrelated species (see Table 12, p. 138). It is most closely related to *C. multipennus*, a species also restricted to New Zealand, but differs from it in having 1) asymmetrically connate underleaves—short and broad on one side and longer and narrower on the other (compare Figs. 51: 1, 4 and Fig. 53: 3); 2) a greater number of cells composing the leaf lobe uniseriate row; 3) plasticity of branch position (see description); 4) smaller leaf cells; 5) leptodermous median and distal cells of the underleaf lamina, with trigones small or altogether lacking (Fig. 51: 11); 6) a higher frequency of leaf armature, with 1(2) processes occurring on at least some leaves of most shoots; and 7) simple or branched paraphyses at the base of the inner or outer surface of ♂ bract lobules (Fig. 51: 6, 7).

Androecial paraphyses, present in *C. helmsianus*, are otherwise rare in Lophocoleaceae. The only other member of the family possessing them is *Pedinophyllopsis abditus* (Sull.) R. M. Schust. & Inoue, a subantarctic species (see Engel, 1990a). The position of paraphyses in *C. helmsianus* is unusual for hepatics.

The species is notable for the pungent odor, which is particularly noticeable with fresh material. The odor is reminiscent to that of a stink beetle. At a station in Westland (*Engel & von Konrat 28439*; see under Ecology), plants occurred on a saturated floor of a forest, and the odor at this site was notable from several meters distance.

VARIATION—Weak populations of the species may offer confusion, in that several sectional criteria are feebly expressed or lacking on some sectors of the population but present on other sectors. *Schuster 67-3201* serves as an example.[6] Underleaves are mostly narrowly connate on both sides, but the side of the underleaf with the long strip of decurrent tissue is attached to the dorsal surface of the leaf base, a rather common condition in better developed material. Some particularly weak shoots have underleaves free on one side. Trigones are small to medium on some shoots. However, other shoots should be checked because they were found to have trigones small in volume but feebly knot-like. Some weak populations may even have minute to small trigones (e.g., *Allison H1399*). Trigones, when optimally developed, are knot-like (Fig. 51: 3)

A suite of diagnostic characters remains even in suboptimal populations. These features are valuable for confirmation purposes and are the frequent dorsal connation of leaves, the distinct tendency for a larger ventral leaf lobe, the tendency for the presence of a cilium on the ventral margin of leaves, and the abundant lateral-intercalary branching. Antheridial stalks are biseriate. That character alone will exclude all of sect. *Lophocolea* from consideration.

NOTE—1) Underleaf connation is asymmetric: a rather broad attachment occurs on the side nearest to a ventral leaf base, but a narrower, longer, and more basal connation occurs on the other. The narrower connation is variable, often on one shoot. If leaf arrangement tends toward opposite, underleaf connation is distinct and rather broad on both sides. If leaf arrangement varies toward alternate, connation occurs via the decurrent strip of underleaf tissue which either fuses with the ventral-basal extremity of the leaf or the dorsal surface of the leaf base. Underleaves are often asymmetrically inserted, and underleaves are oriented toward that side of the shoot with longer, narrower leaf–underleaf connation (Fig. 51: 9). Presumably this is a developmental phenomenon in which tension is asymmetric, being stronger on the side with closer and wider attachment, with resulting torque of the underleaf accompanying shoot elongation.

NOTES ON TYPE SPECIMEN—*Lophocolea helmsiana* Steph. Plants are somewhat lax. Leaf lobes are often missing, but when present have a uniseriate row of 4–7 cells. Trigones are variable even on a single shoot: on one sector they may be small to medium and straight sided, whereas on another sector they may be decidedly knot-like (see sub Variation). Subfloral innovations are abundant, and shoots often repeatedly innovate. The immature and mature gynoecia occur on rather short to long intercalary branches as well as on subfloral innovations. Mature sporophytes are present. The description of the gynoecium and sporophyte in this treatment are based largely on this collection.

DISTRIBUTION AND ECOLOGY—Known from scattered, rather few stations in New Zealand (South Is., 50–365 m; North Is., 150–1100 m), where the species occurs in very wet, deep, rich forests. The species mostly occurs on tree fern trunks, rotted logs, and, less often, shaded rock and banks. At Lee Bay on Stewart Is., plants occurred on the trunk of *Dicksonia squarrosa* at 5 m above sea level directly above shoreline in very exposed coastal scrub, including *Brachyglottis rotundifolia*, *Carpodetus serrata*, and *Coprosma robusta* at the margin of a podocarp/hardwood forest. At a station in Westland (SH 6 opposite junction of Woodstock and Rimu Road; *Engel & von Konrat 28439* referred to above) plants occurred at 40 m on a saturated floor of a regenerating thicket of *Dacrydium cupressinum* and *Metrosideros umbellata* and pockets of *Cortaderia* and *Blechnum* at the margins.

It is interesting to note that *C. helmsianus* is apparently lacking from North Auckland, whereas the related *C. multipennus* extends north to the Waipoua kauri forests in North Auckland.

SPECIMENS SEEN—**NEW ZEALAND. STEWART ISLAND:** Lee Bay, at head of Rakiura Track to Christmas Hut, ca. 3 km N of Oban, 5 m, *Engel, von Konrat & Braggins 24095* (F). **SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, Tutoko River Valley, near head of Milford Sound, *Schuster 67-2791* (F). **OTAGO:** Mt. Cargill, N of Dunedin, ca. 365 m, *Child H 1344* (F). **WESTLAND:** Directly opposite junction of Woodstock and Rimu Road on SH 6, 40 m, *Engel & von Konrat 28439* (F); Greymouth, *Helms s.n.* as

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[6] The locus and date of collection for *Schuster 67-3201* is identical to that of better developed material of the species, such as *Schuster 67-4163*.

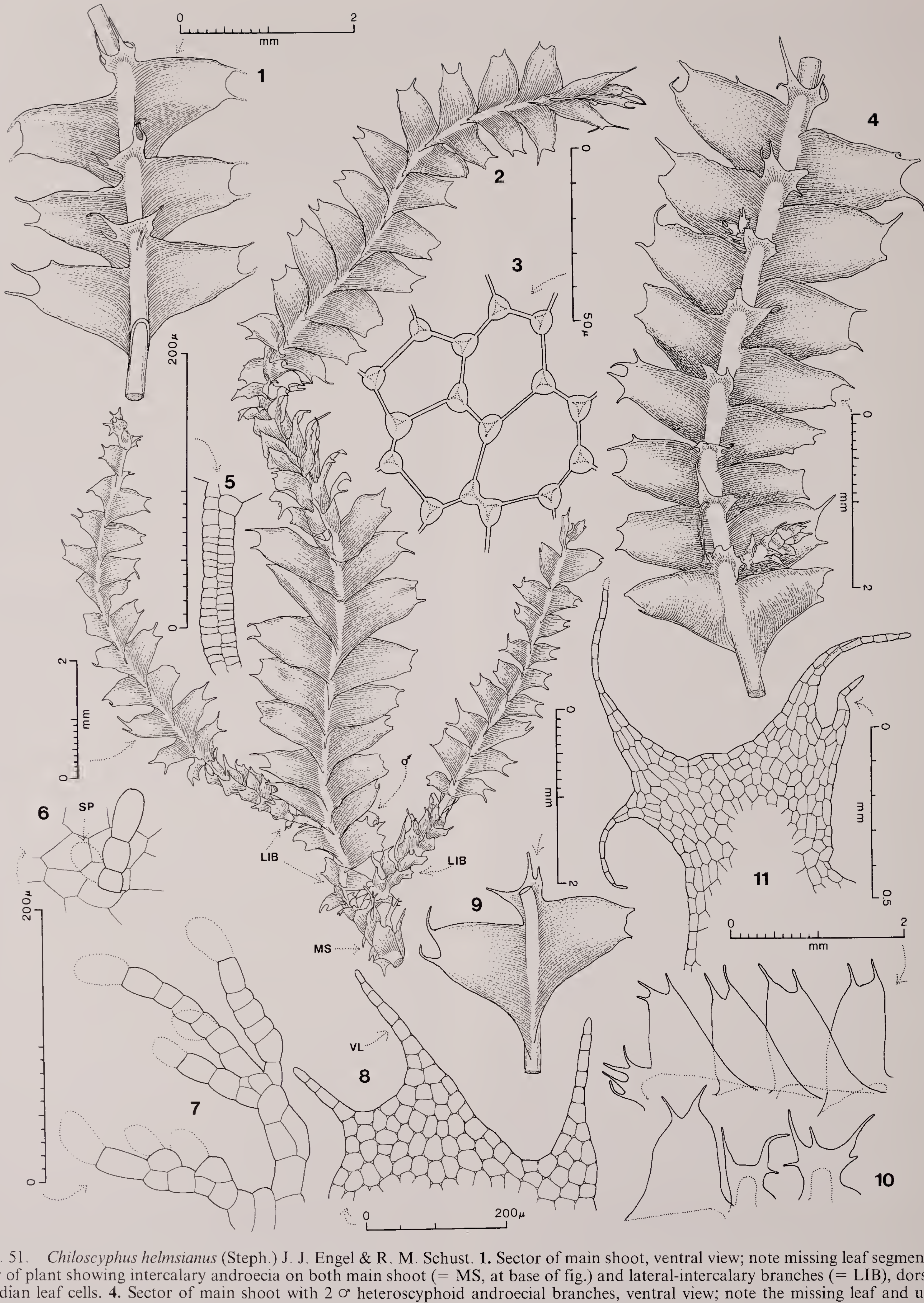

FIG. 51. *Chiloscyphus helmsianus* (Steph.) J. J. Engel & R. M. Schust. **1.** Sector of main shoot, ventral view; note missing leaf segment tips. **2.** Sector of plant showing intercalary androecia on both main shoot (= MS, at base of fig.) and lateral-intercalary branches (= LIB), dorsal view. **3.** Median leaf cells. **4.** Sector of main shoot with 2 ♂ heteroscyphoid androecial branches, ventral view; note the missing leaf and underleaf segment tips, the variation of apex and margin armature and that larger androecium is basal. **5.** Antheridial stalk. **6, 7.** Reduced and well-developed paraphyses of inner face of ♂ lobule (sp = slime papilla). **8.** Distal sector of leaf (vl = ventral lobe). **9.** Opposing leaves and attached underleaf. **10.** Leaves and underleaves. **11.** Underleaf. (**6,** from *Schuster 67-3172*, New Zealand, North Is., Urewere Natl. Park, Whakataka Track; remainder from *Schuster 3163*, same loc.)

L. subporosa–c. sporo. (M). **NELSON:** Little Totara River, 90 m, *Child H3617*–c. per. + ♂ (F). **NORTH ISLAND. HAWKE'S BAY:** Near Wairoa, *Hatcher 1271* (F). **GISBORNE:** Lake Waikaremoana, *Hodgson 626* (CHR). **GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY:** Urewera Natl. Park, Whakataka track, from NS road toward Mt. Whakataka Mtn., 945–1100 m, *Schuster 67-3163*, *67-3172*–c. per. + ♂, *67-3201* (F). **SOUTH AUCKLAND:** Near Atiamuri, S of Rotorua, *Allison H 538* (CHR); Puaiti Bush, S of Rotorua, *Allison H 3439* (CHR); on coast side of Lake Rotoehu, Bay of Plenty, *Allison H 616* (CHR); between Lake Rotoehu and the coast, Bay of Plenty, ca. 150 m, *Allison H 3406* (CHR); Coromandel State Forest Park, Kauaeranga River, just SE of suspended footbridge, 150 m, *Engel 22303*–c. per. (F).

Chiloscyphus multipennus (Hook. f. & Taylor) J. J. Engel & R. M. Schust.

Jungermannia multipenna Hook. f. & Taylor, London J. Bot. 4: 81. 1845. *Lophocolea multipenna* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 699. 1847. *Chiloscyphus multipennus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 419. 1985 (1984). Lectotype (*fide* Engel, 1991b): Auckland Is., *Hooker* (FH!–c. per. + ♂); (isolectotypes: BM![3]–c. per. + ♂).

Lophocolea pallida Mitt. *in* Hooker f., Bot. Antarc. Voy. 2: 135. 1854, *syn. cf.* Hooker (1864–67), *non L. pallida* Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(7): 80. 1876. *Chiloscyphus pallidus* (Mitt.) J. J. Engel & R. M. Schust. Nova Hedwigia 39: 420. 1985 (1984). Type: New Zealand, North Is., Auckland, *Sinclair s.n.* (NY!).

Chiloscyphus involucratus Colenso, Trans. & Proc. New Zealand Inst. 22: 455. 1890 (1889) ("*involucrata*"), *syn. nov.* Type: New Zealand, [Waipawa Co., south of Dannevirke, 1889], *Colenso a. 1516* (BM!–c. sporo., G = *absens*, WELT = *absens*, Y = *absens*).

Lophocolea erectifolia Steph., J. Linn. Soc., Bot. 29: 269. *pl. 27, f. 12–15.* 1892, *syn. fide* Hodgson (1953). *Chiloscyphus erectifolius* (Steph.) Steph., Bull. Herb. Boissier 8(2): 147. 1908 (= Spec. Hep. 3: 263), *nom. inval.* (Art. 33). Lectotype (*nov.*): New Zealand, North Is., without specific locality, *Colenso 1701* (G!–c. sporo.+ ♂) (isolectotype: BM!–c. ♂).

Lophocolea zuernii Steph., Bull. Herb. Boissier 6(9): 795. 1906 (= Spec. Hep. 3: 95) ("zürnii"), *syn. nov.* Lectotype (*nov.*): New Zealand, North Is., Prov. Auckland, near town of Coromandel, March 1882, *Zürn 23* (G!, "original").

Plants soft and rather flexuous, creeping to somewhat ascending, pale green (pale olive green in herb.), nitid when dry; shoots to 3 mm wide, rarely to 3.6 mm wide. Branches common, nearly exclusively of lateral-intercalary type, consistently from "axil" of leaf–underleaf connation; *Frullania*-type branching very rare (only 1 branch seen). Stems rather narrow for plant size, 13–16 cells high, the cortex poorly differentiated laterally and dorsally, in 1 row of slightly smaller cells with slightly thickened walls, the ventral cortical cells moderately well differentiated, in 2–3 layers of moderately thick-walled cells that are somewhat smaller than the thin-walled medullary cells. Rhizoids long for shoot size, dense at immediate base of underleaf but often becoming scattered and less dense on ventral face of stem, the tips often branched. Leaves subopposite, grading from horizontal to somewhat dorsally assurgent, spreading at right angles or nearly so, imbricate and if densely so, then each leaf overlapping (or overlapped by) sectors of the next 2 leaves both above and below (i.e., 4 in all, and seen optimally on well-developed sterile shoots), the leaves free dorsally, orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement covering much of stem in dorsal view but V-shaped sectors of stem tissue left exposed. Leaves convex, asymmetrically ovate to subdeltoid, clearly widest near base; apex commonly consistently bifid to 0.07–0.17, the apices often variable and then bidentate-lobate to 1-dentate-lobate to retuse to undivided and rounded; lobes usually parallel to slightly diverging, of ± equal size or the ventral sporadically larger (but never consistently larger than the dorsal), narrowly acute to acuminate, terminating in a uniseriate row of 2–4 cells that are isodiametric or slightly longer than wide, the lobe margins entire, the sinus rounded; dorsal margin straight to slightly and gently curved, plane to deflexed, entire, short to rather long decurrent; ventral margin broadly and conspicuously arched, often dilated in basal sector, always more strongly arched than the dorsal, plane, usually entire, rarely with a tooth. Leaf cells smooth, often dimorphic: most thin walled and with bulging and knot-like trigones, but scattered among them are cells with walls ± evenly secondarily thickened and with trigones ill-defined; median cells 30–42 μm wide, 35–49 μm long; surface smooth or finely papillose. Median and distal cells of underleaf lamina with trigones medium to knot-like. Underleaves much smaller than leaves, *in situ* 1.5–2.4× stem width (see Note 1), very broadly and symmetrically connate on both sides, the insertion inverted U-shaped, the underleaves slightly spreading, contiguous to imbricate, those of well-developed shoots covering stem except for U-shaped patches at each underleaf base, concave, especially near base (ventral view), the margins recurved (particularly near the base), but the apex oriented toward shoot apex, subquadrate to obtrapezoid, the apex ± truncate, 4-lobed in well-developed phases, 2–4-lobed in suboptimal plants, the lobes acuminate to subcaudate and of about equal size, the median pair ± parallel to slightly diverging, the lateral pair with orientation varying from parallel with median lobes to ca. 90° to stem, the lobe margins entire (very rarely and sporadically with a tooth or cilium) and terminating in a uniseriate row of 2–6(7) cells, the median sinus descending to 0.55–0.7, the lateral pair of equal depth, or, in suboptimal plants, the median sinus shallower and then the outermost processes appear apical-lateral or lateral in position (the underleaves then appear bifid), the apex and lamina margins otherwise lacking other armature except for a rare and sporadic cilium or lacinium on the margin that defines the sinus.

Asexual reproduction absent.

Plants dioecious; ♂ and ♀ plants at times closely intermingled. Androecia often produced in abundance, on leading shoots or elongate, indeterminate, lateral-intercalary branches, the androecia initially terminal but eventually become intercalary, often on short abbreviated branches without subtending vegetative leaves (the androecia then ± heteroscyphoid) but at other times proliferating vegetatively distally (the androecium then basal on a lateral branch), subfolious to spicate, often composed of numerous (up to 17) bract pairs. Bracts somewhat to markedly smaller than leaves, spreading, vertical, strongly dorsally assurgent, tightly appressed to bract immediately above, the saccate portion crenulate in profile and fused toward base with opposite bract, the bracts ventricose in basal portion, the distal portion stiffly vertical (particularly on spicate androecia) to reflexed, the apex short bifid, the ventral margin entire; lobule margin involute, irregularly crenate-dentate but also with a few ciliiform projections, copious slime papillae and a conspicuous tooth in distal sector; antheridia solitary, large for bract size, the stalk biseriate. Gynoecia somewhat *Plagiochila*-like and spiny in appearance, on main shoot or lateral-intercalary branches of variable length: reduced, abbreviated and lacking normal vegetative leaves or longer and with a few to several cycles of normal leaves, the gynoecia very rarely (1 branch seen) on long

TABLE 12. Comparison of characteristics of *Chiloscyphus multipennus*, *C. helmsianus*, *C. trialatus*, and *C. suboppositus*.

Character	*C. multipennus*	*C. helmsianus*	*C. trialatus*	*C. suboppositus*
Stem tissue exposed in dorsal view	V-shaped sectors (Fig. 52: 6)	V-shaped sectors (Fig. 51: 2)	V-shaped sectors (Fig. 57: 7)	narrow strips (Fig. 55: 1)
Leaf symmetry	ventral margin more arched than dorsal, frequently dilated (Fig. 53: 4)	margins subsymmetrically arched or the ventral somewhat more curved (Fig. 51: 10)	ventral margin often more arched than dorsal, frequently dilated (Fig. 57: 12)	ventral margin often less arched than dorsal (Fig. 55: 13)
♂ Lobule armature	1- or more-celled tooth distally (Fig. 54: 13)	dentiform to laciniiform process distally	2–4 teeth	multicellular tooth distally
♂ Position (other than main shoot)	lateral-intercalary branches	lateral-intercalary branches	terminal and lateral-intercalary branches	lateral-intercalary branches
Heteroscyphoid-type androecia	often present	often present	often present	lacking; (♂ uniformly on leading shoots)
♂ Bracts	subfoliose to spicate	subfoliose to spicate	subfoliose to spicate	subfoliose
Perianth lobes	caudate (Fig. 54: 5)	caudate	commonly caudate (Fig. 58: 7)	narrowly acute to subacuminate (Fig. 56: 4)
Capsule wall inner layer	fenestrae lacking (Fig. 54: 9)	fenestrae lacking	fenestrae sporadic (Fig. 58: 1)	fenestrae well developed (Fig. 56: 3)
Capsule wall: radial walls of outer layer	continuous sheets lacking (Fig. 54: 10)	—	continuous sheets feeble and irregular	continuous sheets well developed (Fig. 56: 10)
Spore size (µm)	8.2–9.6	10.1–11	9.6–11	12–15

Frullania-type branches; vestigial stem perigynium present, the bracts and bracteoles of at least the innermost 2 series inserted on the vestigial perigynium. Bracts crowded, the insertions close to one another, the bracts of innermost series moderately to distinctly larger than leaves, suberect to erect and ensheathing at least the base of the perianth, free from one another, convex (often strongly so), ovate; apices bifid to 0.05–0.1, the ventral lobe larger, the lobe margins entire; dorsal margin deflexed, often abruptly and strongly so and forming a weak cnemis, with up to 11 spinose teeth in middle third or, occasionally, entire; ventral margin deflexed, sparingly to copiously armed with spinose teeth and laciniae. Bracteoles of innermost series somewhat smaller than bracts, at times subequal to bracts in length but narrower, normally connate on both sides and often broadly so, exceptionally free on 1 side and connate on the other, concave (ventral view), ovate to subquadrate; apices 2–4-fid to 0.2–0.25, the lobe margins entire or with a few spinose teeth or laciniae, the sinuses of about equal depth; lamina margins entire or, on bifid bracteoles, on each side with a spinose dentiform-laciniiform process. Perianth barely to moderately exserted beyond bracts, sharply trigonous throughout, ventral and lateral sides often infolded, the perianths short obovate-campanulate to short oblong, not narrowing toward mouth, frequently bilaterally compressed because of infolded lobes, deeply 3-lobed, the lobes free for ca. 0.4–0.5 the perianth length; lobes distinctly truncate, deeply bifid, the segments caudate, usually entire but occasionally with a laciniiform process, the lobes otherwise with numerous accessory acuminate laciniae and spinose teeth; keelar wings common, conspicuously high, to 0.5 the perianth width, high and decurrent on the vestigial perigynium, the free margin spinose dentate to laciniate.

Seta seen only in collapsed state. Capsule elliptic, 700 µm × 490 µm, 32–37 µm thick, of 5–6 layers, the outer layer of cells equal to thickness of 2.2–2.8 of interior strata; outer layer of cells subquadrate to subrectangular, the radial walls thin to somewhat thickened locally, the walls with magenta nodular to occasionally feebly spine-like thickenings that are mostly on longitudinal walls and sometimes on transverse walls, the longitudinal and transverse walls lacking continuous sheets of pigmented material; innermost layer of cells long and narrowly rectangular, the longitudinal radial walls with thin continuous sheets of red-brown material, with semiannular bands red brown, common, rather wide, usually complete, rather commonly forked but not anastomosing to delimit fenestrae, the radial walls with nodular or spine-like thickenings lacking on both longitudinal and transverse walls.

Spores 8.2–9.6 µm, pale brown, very thin, with faint low, close papillae and short vermiculate markings, spore:elater diameter ratio 1.1–1.3:1. Elaters weakly tortuous, 7.2–7.7 µm wide, the spirals 1.9–2.4 µm.

DIFFERENTIATION—*Chiloscyphus multipennus* has been confused with *Heteroscyphus cuneistipulus*, and understandably so, in that the two species have a superficially similar appearance. Careful search should be made for heteroscyphoid-type sex organs, which are commonly present and will immediately distinguish *H. cuneistipulus*. In the absence of these, *H. cuneistipulus* has leaf lobes subcaudate or piliferous, underleaves on each side only narrowly connate, leaf cell trigones small, leaf margins sometimes with a cilium on the dorsal, ventral, or both margins, and with the margin defining the underleaf sinus lunate and often bearing 1–2 cilia.

This species is allied to *C. helmsianus*, *C. suboppositus*, and *C. trialatus*. The main distinguishing, as well as inter-relating, features of these species are shown in Table 12. Characters to distinguish *C. multipennus* and *C. helmsianus* are discussed under the latter species (p. 135).

VARIATION—In some populations the leaf lobes are nearly all symmetrical—the ventral about equal to the dorsal in stature (Fig. 53: 4). In other populations one finds a mixture of some leaves with subequal lobes and other leaves that have a somewhat larger ventral lobe. Lobe symmetry is of diagnostic value in that the allied *C. suboppositus* has ventral lobes consistently larger than the dorsal (Fig. 55: 1, 2, 12). Interestingly, female bracts of *C. multipennus* consistently have larger ventral lobes (Fig. 54: 3, 4).

Weaker phases of the species, such as *Hatcher 429*, should be treated with care since several of the more obvious characters present in well-developed plants are lacking or poorly expressed. For example, underleaves are weakly concave (in ventral view) or even plane, and often bilobed, the lateral pair of processes being reduced. Furthermore, underleaves are contiguous rather than decidedly imbricate, and allow exposure of elongate sectors of stem tissue. Also, although leaves with subequal lobes are present in weaker plants, there is greater frequency in such plants for leaves with larger ventral lobes.

Engel 18731 from Fiordland Natl. Park is an interesting variant. It deviates from the usual condition in having some shoots with variable leaf apices. The apex variation ranges from bilobed to 2-dentate to 1-dentate/lobate to retuse to undivided and broadly rounded. This variation commonly occurs on one shoot (Fig. 53: 8). Other intermixed shoots have leaves consistently bilobed, the condition typical for the species. Some of the variable-leaved shoots are particularly robust for the species, and may be up to 3.6 mm wide. Some populations consist entirely of shoots with variable leaf apices.

NOTES—1) Underleaf width was obtained by measurement between bases of opposing lateral lobes. The base of the lateral lobe was obtained by drawing a line that bisected the crotch between leaf and underleaf (connation tissue) and the sinus base between the apical and lateral lobes. This is effectively the width of the discus.

2) Some collections are nearly exclusively androecial or gynoecial-androecial, with sterile shoots rare. In such cases gyres well removed from sex organs should be utilized for nonreproductive characters.

3) Rodway (1916) recognized *L. erectifolia*, included a diagnosis that compared with Stephani's (1892) protologue of that species, and cited Mt. Wellington and New Zealand for provenance. All four specimens of *L. erectifolia* seen from HO are actually *C. perpusillus*—three are from Mt. Wellington (two determined by Stephani, one by Rodway) and the fourth from National Park. *Chiloscyphus multipennus* (= *L. erectifolia*) does not occur in Tasmania.

4) Hodgson (1953, p. 345) included the monoecious *C. trialatus* in her concept of *L. pallida* (*teste* numerous collections at CHR all labeled either *L. multipenna* or *L. pallida*). That accounts for her statement that *L. pallida* is "polyoicous" and has an "ofttimes monoecious inflorescence."

5) All collections from Snares Is. are small and compact and have leaves that are somewhat wider than usual.

6) The name *Jungermannia multipenna* was originally published in Hooker and Taylor (1844, p. 381). However, as pointed out by Hooker and Taylor (1845, p. 81), "by an accidental error" the description and comments found on p. 381 of the 1844 paper are an exact replication of those for *Jungermannia* (*Isotachis*) *intortifolia* (which was published by Hooker and Taylor [1844, p. 381]).

NOTES ON TYPE SPECIMENS—1) *Jungermannia multipenna* Hook. f. & Taylor. See Engel (1991b).

2) *Lophocolea pallida* Mitt. The specimen represents a well-developed phase of the species; Figure 52 is based on original material at NY. The plants are dioecious.

3) *Chiloscyphus involucratus* Colenso. The only specimen I was able to locate is at BM; it consists of several shoots: one sporophyte-bearing, the remainder sterile. The specimen represents a somewhat atypical phase of *C. multipennus*.

The collection agrees with *C. multipennus* in most respects. The leaf lobes are narrowly acute to acuminate and the ventral (= "upper horn") is commonly longer (and larger), as noted in the protologue. Perianths have high-armed wings and are deeply 3-lobed, the lobes being deeply bifid by caudate segments. The gynoecium occurs on a rather short lateral-intercalary branch consisting of 3 series of bracts and bracteoles subtended by 3 leaf gyres. That gynoecial position and branch length often occurs in *C. multipennus*. Gynoecial features appear similar to those illustrated in Figure 54: 2, 3, and 5.

The specimen has some features usually not expressed in well-developed *C. multipennus*. Trigones are variably expressed, even on leaves of the same shoot–some are small, whereas others are knot-like. The suboptimal trigone development is likely because the plant is a shade form. (The protologue states for habitat only that the plant occurred in "low wet woods.") The ventral margin of the leaf occasionally has 1–2 cilia; ventral margin armature normally is rare in *C. multipennus*. Four vegetative branches are present: one is terminal, the others lateral intercalary. This is the only terminal branch observed for *C. multipennus*.

4) *Lophocolea erectifolia* Steph. Original material consists of well-developed plants with mature sporophytes, knot-like trigones, and underleaves ca. 0.75–0.85-fid and broadly connate on both sides; the specimen is dioecious, as stated by Stephani (1892). Sporadic underleaves have an accessory cilium or lacinium on lobe margins or on the margin defining the median sinus. Underleaves normally are devoid of all armature other than lobes and the pair of lateral/terminal processes.

5) *Lophocolea zuernii* Steph. A statement on the first line of the protologue reads "typus in herb. Stephani." I have seen all three specimens labeled *L. zuernii* on deposit at G. Two are labeled *Zürn* no. *23*, and though label data is not identical, the date and locality match. The two specimens, however, differ in presence of fertile structures. The collection with "original" written on the packet face has an isolated male branch (overlooked by Stephani) but is otherwise sterile. The packet face, however, is marked "c. fr.," and perhaps the piece bearing perianths was segregated and either constitutes the material of the other Zürn collection at G or is on deposit elsewhere. The specimen contains a careful dissection of a gyre; Stephani illustrated a gyre in his icone of the species (*Lophocolea* no. 144). The second specimen bears mature sporophytes, which conflicts with Stephani's statement that perianths are juvenile. The Stephani icone of the species includes a figure of a perianth labeled as juvenile. That figure is unlike perianths that bear mature sporophytes in the Zürn specimen but agrees with the protologue. The protologue also cites Colenso as a collector. I have seen a New Zealand Colenso specimen (G *24421*) with young gynoecia, but perianths differ from both protologue and icone. The origin of perianth data in the protologue is unknown but may have been obtained from a segregate of the *Zürn 23* specimen that is not at G. It is perhaps possible that perianths were erroneously described as immature, when they actually are mature. In support of that statement, the perianth figured in the icone compares in several respects to the mature perianth illustrated in Figure 54: 5. I am treating the two Zürn collections as parts of a single specimen that was subdivided. Because plants from the collection marked "original" match the protologue (with the exception of perianth data), I have designated that specimen as lectotype. I am treating the other Zürn specimen as an isolectotype. It should be noted that the species was

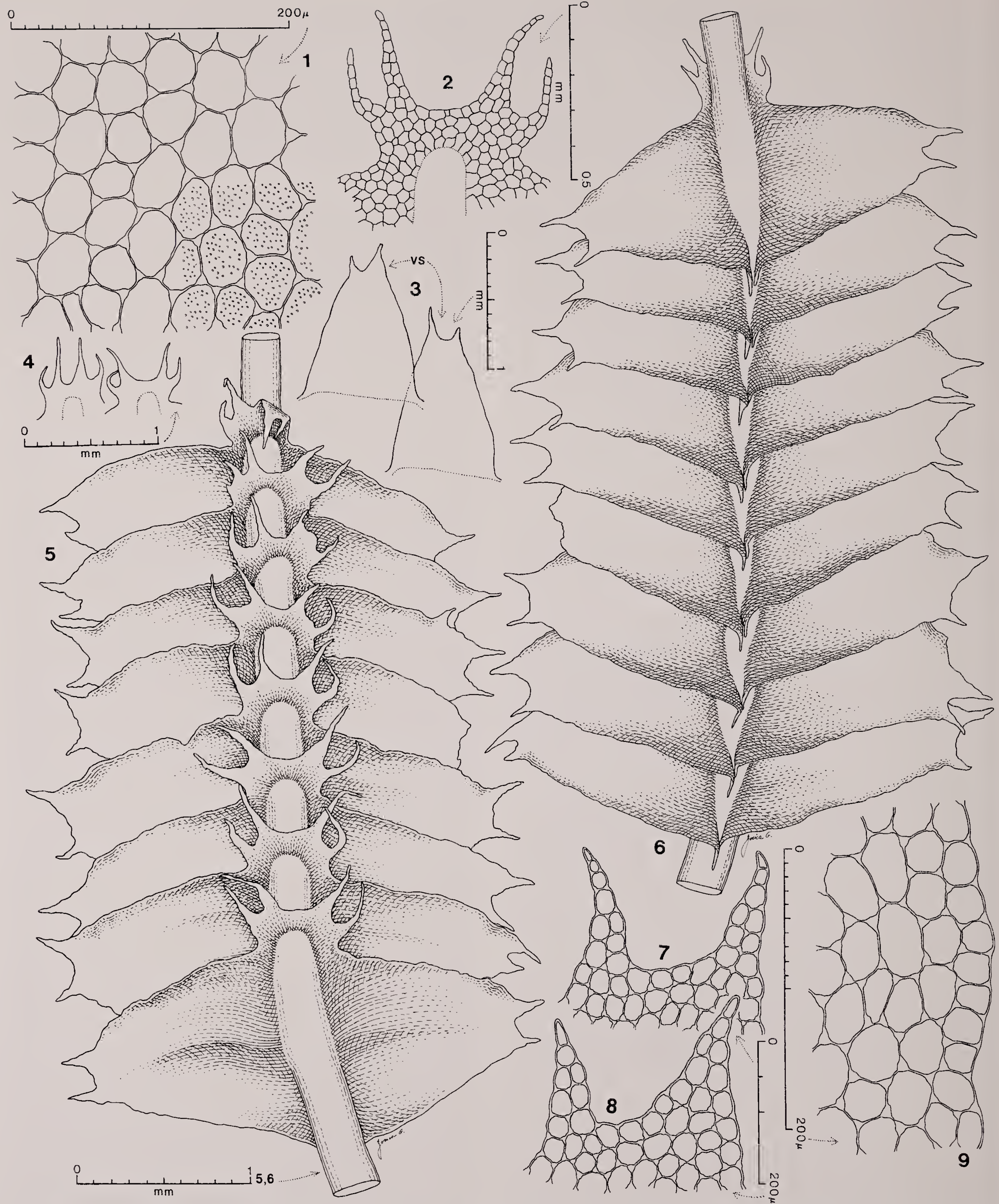

FIG. 52. *Chiloscyphus multipennus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **1.** Median leaf cells (note slightly roughened cuticle). **2.** Underleaf. **3.** Two leaves (vs = ventral segment). **4.** Two underleaves. **5.** Shoot, ventral view. **6.** Shoot, dorsal view. **7, 8.** Distal sectors of leaves. **9.** Marginal cells of leaf. (All from type of *Lophocolea pallida* Mitt. [NY].)

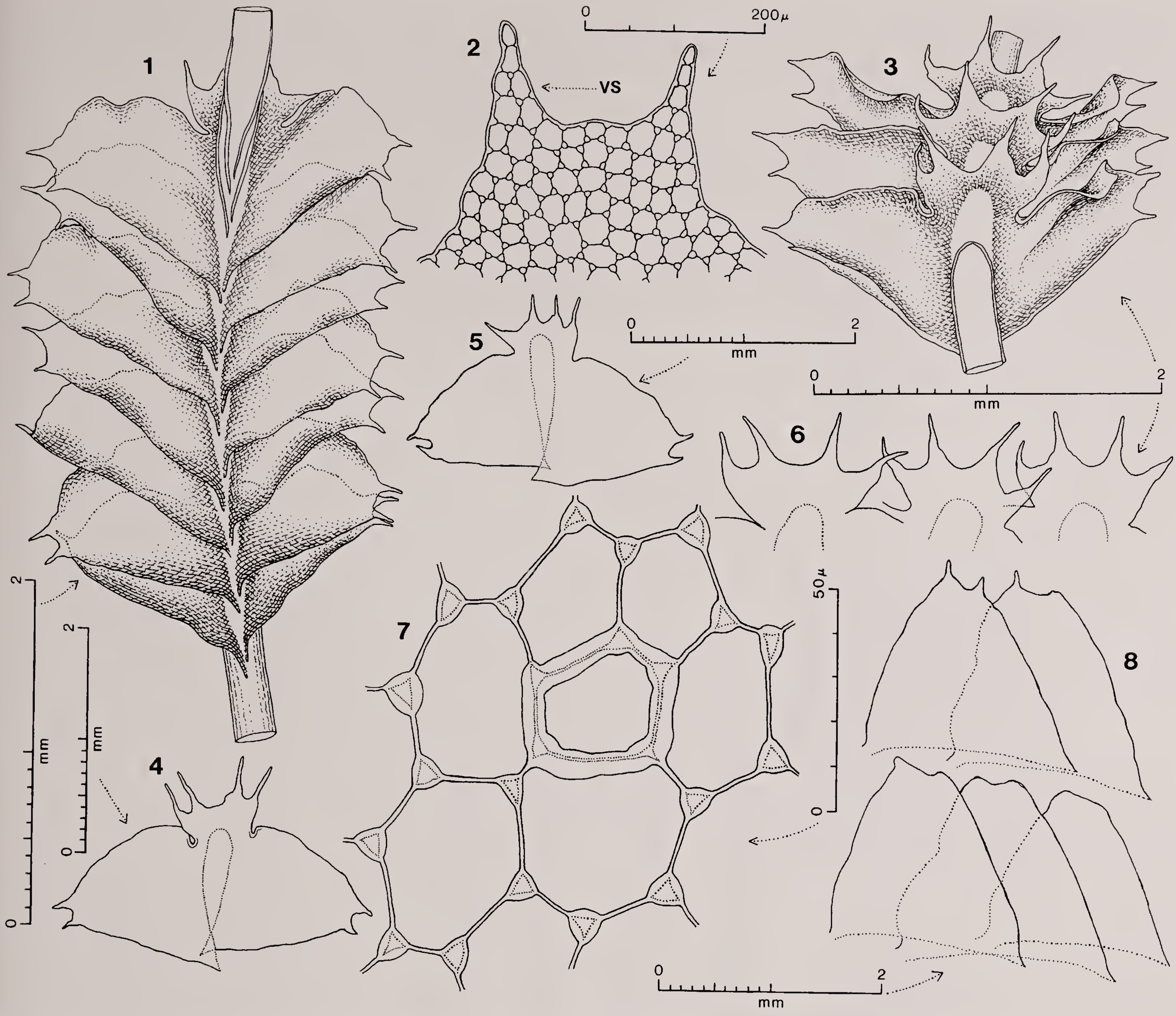

FIG. 53. *Chiloscyphus multipennus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **1.** Sector of main shoot, dorsal view; note that each leaf covers portions of 4 others: 2 above and 2 below; note also high frequency of symmetric leaf lobes. **2.** Distal sector of leaf (vs = ventral segment). **3.** Sector of main sterile shoot, ventral view. **4, 5.** Opposing pairs of leaves each with attached underleaf. **6.** Underleaves. **7.** Median leaf cells, note cell dimorphism. **8.** Leaves from one shoot; note apex variability. (**1, 4,** from *Hatcher 444*, New Zealand, North Is., Waipoua Kauri Forest; **2, 3, 5–7,** from *Hatcher 505*, same loc.; **8,** from *Engel 18731*, New Zealand, South Is., above South Branch of Borland Burn.)

named after Zürn, and in such cases of eponymy (especially with Stephani names) it is preferable that the epithet agree with collector, unless evidence exists to the contrary. At times this is impossible, as in *L. goebeliana*.

Lectotype plants are well-developed, with knot-like trigones, underleaves broadly connate on both sides, and leaf lobes with a uniseriate row of 2(3) cells.

DISTRIBUTION AND ECOLOGY—Auckland Is., New Zealand (South Is., 15–680 m; North Is., 95–305 m), and Snares Is. It has a bimodal distribution in New Zealand, occurring in Southland and Otago Provinces on South Is. and South Auckland and North Auckland Provinces on North Is. (one station in Nelson Prov. being the only exception).

The species occurs nearly exclusively on decayed logs (and is only sporadically terricolous) in forests, such as in *Nothofagus* forests of South Is. and mature *Agathis*-hardwood forests (e.g., at Waipoua) of North Is. On Auckland Is. it occurs on the bases of *Poa littorosa* tussocks and on Snares Is. on damp, shady peat and rootlets under *Olearia lyallii*, on fallen, rotted *O. lyallii* and over peat in abandoned penguin colonies.

SPECIMENS SEEN (selected)—**AUCKLAND IS.:** French Islet, Port Ross, *Fineran 1572*–c. per. + ♂ (CHR). **NEW ZEALAND.** Without specific loc., *Colenso 944, 1622, 1646, 1838*, all as *L. erectifolia* (BM); ibid., *Petrie s.n.* as *L. subporosa* (G); ibid., *Petrie 75* as *L. subporosa* (CHR). **SOUTH ISLAND. SOUTHLAND:** Bluff Hill, *Allison H 5167* as *L. pallida* (CHR); Table Hill Scenic Reserve, Puketiro Road, Papatowai Highway, 250 m, *Engel, von Konrat & Braggins 23974*–c. per. + ♂ (F); Lake Hauroko, ca. 120 m, *Child H 1558*–c. sporo. + ♂, *1563* (F); Fiordland Natl. Park, 11.3 km by road WNW of Borland Lodge, above S branch of Borland Burn, W of Monowai, 680 m, *Engel 18731*–c. sporo. + ♂ (F). **OTAGO:** Catlins district, bush behind Tantuku Beach, *Allison H 6358* as *L. pallida*–c. per. + ♂ (CHR); Akatore, 20 mi. SW of Dunedin, 15 m, *Child 987* (F); E face of Maungatua Range, ca. 550 m, *Allison H 1395*–c. per. + ♂, *H 1396* as

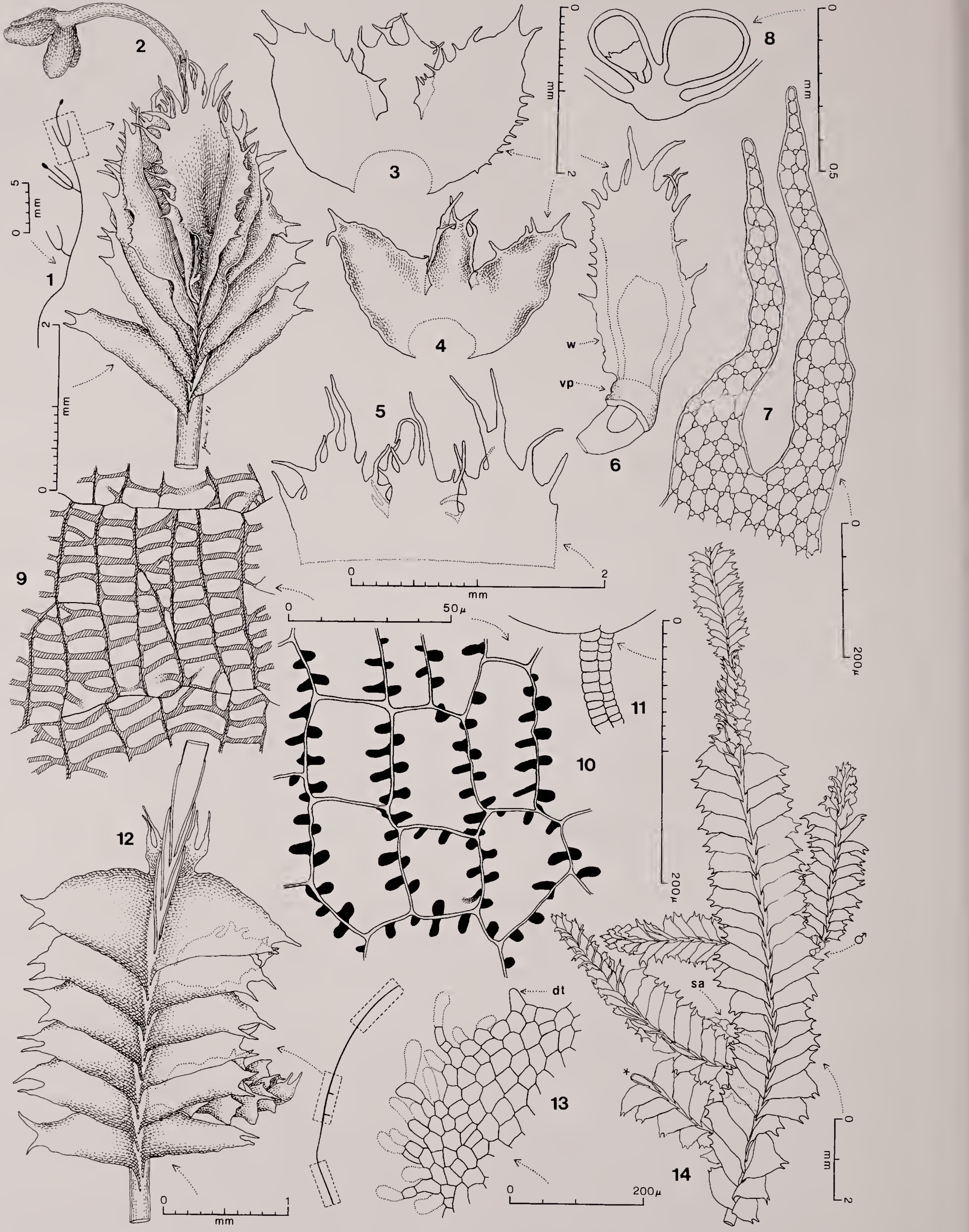

FIG. 54. *Chiloscyphus multipennus* (Hook. f. & Tayl.) J. J. Engel & R. M. Schust. **1.** Cladograph of shoot with 3 perianths, the distal 2 with mature sporophytes, the basal one mature but without a sporophyte, the lower 2 gynoecia on short lateral-intercalary branches lacking vegetative leaves (distal sector with stipple boundary drawn in detail in **2**). **2.** Gynoecium with dehisced capsule, dorsal view (sector indicated in **1** drawn in detail). **3, 4.** ♀ Bracts and in middle, bracteole, abaxial view; at top, flattened, at bottom, somewhat flattened; note difference in armature. **5.** Perianth mouth, ventral lobe in middle. **6.** Lateral face of perianth (w = wing; vp = vestigial perigynium, the base of which is shown in longisection). **7.** Distal sector of lateral lobe of perianth. **8.** Opposing antheridial bracts with stem, cross section; note dehisced antheridium. **9.** Capsule wall, inner layer. **10.** Capsule wall, outer layer. **11.** Antheridial stalk. **12.** Sector of main shoot with 2 spicate androecia, one hidden by

L. pallida–c. ♂ (CHR); Leith Valley Road, Dunedin, ca. 455 m, *Allison H 5491* as *L. pallida* (CHR); Mt. Aspiring Natl. Park, Makarora River, at base of Haast Pass, *Allison H 5977* as *L. pallida*–c. per. (CHR). **NELSON:** Lake Rotoroa, *Simpson s.n.* as *L. pallida*–c. sporo. + ♂ (CHR). **NORTH ISLAND. SOUTH AUCKLAND:** Oruanui Bush, near Taupo, *Allison H 3386*–c. sporo. + ♂ (CHR); near Oruanui, N of Taupo, *Allison H 544*–c. ♂ + per. + sporo. (CHR); Rainbow Mtn., S of Rotorua, ca. 305 m, *Allison H 5129* as *L. pallida* (CHR). **NORTH AUCKLAND:** McElroys Bush Reserve, western side of Mahurangi Harbour on Cowan Bay Road, 95 m, *Engel 20387*–c. per. + ♂ (F); Waipoua Kauri Forest, *Hatcher 429*–c. ♂ + per., *505*–c. ♂ + sporo. (F); Waipoua Forest, *Allison H 710* as *L. pallida*–c. sporo. + ♂, *H 745* as *L. helmsiana*, *H 751*, *H 1609*, *H 1620* as *L. pallida* (CHR). **SNARES IS.:** *Horning SA 247* as *L. subporosa* (CHR); *Newcombe s.n.* as *L. pallida*–c. per. (CHR); S promontory, *Horning SA 208* as *L. subporosa* (CHR); near tip of SW promontory, *Horning SA 42*–c. ♂ (CHR); head of Penguin Creek, *Horning SA 18* (CHR); Muttonbird Creek, *Horning SA 17*–c. sporo. (CHR).

Chiloscyphus suboppositus J. J. Engel

Chiloscyphus suboppositus J. J. Engel, Phytologia 83: 45. 1998 (1997). Holotype: Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park, Pine Valley, Cephissus Falls, NNW of Lake St. Clair, 850 m, *Engel 14247*–c. sporo. (F); isotype: (HO).

Plants flexuous but not especially soft, loosely prostrate to ascending, light green, darker toward base, opaque, sometimes rather water repellent, nitid when dry; shoots to 5 mm wide. Branches common, nearly exclusively of lateral-intercalary type, the collar high, rarely and sporadically of *Frullania* type; branches commonly innovating from unfertilized gynoecia. Stems 14–16 cells high, the cortex moderately differentiated, in 1–2 layers of rather thick-walled cells, the differentiation especially pronounced on ventral side of stem. Rhizoids in tight fascicles from stem at immediate base of underleaves. Leaves subopposite, horizontal, widely spreading, loosely imbricate, free or weakly connate dorsally, the orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement practically covering the stem in dorsal view except for very narrow strips. Leaves convex, asymmetrically ovate to subdeltoid, clearly widest near base; apex fundamentally short bifid, but with the ventral lobe much larger than the dorsal, which is distinctly basal in juxtaposition to the ventral lobe (lobes rarely and sporadically subequal), the lobe margins entire; ventral lobe medium acute to acuminate, sometimes apiculate, terminating in a uniseriate row of 1–3, at most, slightly elongated cells; dorsal lobe grading from a laciniiform projection to a small tooth to a low rounded projection; dorsal margin broadly and gently rounded, deflexed, sometimes abruptly and strongly so and forming a weak cnemis, entire, long decurrent; ventral margin straight to slightly rounded, often less strongly curved than the dorsal, the ventral margin broadly and gently deflexed, aligned apical-ventral or ventral, normally entire but rarely and sporadically with a tooth. Leaf cells smooth, without protuberances of any sort, with walls thin, trigones medium to (more often) large and bulging to knot-like, median leaf cells 25–34 µm wide, 40–48 µm long. Underleaves with median and distal cells of lamina with trigones medium to knot-like. Oil-bodies occupying fraction of cell volume, hyaline and glistening, 3–5 to 5–9 per cell, coarsely papillose, globose to subglobose grading to broadly elliptic, often narrowly elliptic and then the shape occasionally a bit irregular, the globules 2.6–3.3 µm in diam., the oil-bodies 7.2–13 × 4.6–5.9 µm, globose ones 5.5–6.5 µm in diam., the subglobose ones 5.9–7.2 × 5.2–5.9 µm. Chloroplasts much smaller than oil-bodies, 3.3 × 1.3–2 µm. Underleaves somewhat like those of *C. tuberculatus* in appearance, much smaller than leaves, *in situ* 2–3.4× stem width, very broadly connate on both sides and usually with an angulation at juncture of leaf and underleaf, the insertion inverted U-shaped, the underleaves slightly to moderately to sporadically strongly spreading, contiguous to loosely imbricate, concave, particularly toward the base (ventral view), the margins reflexed but the apex oriented toward shoot apex, the underleaves subquadrate to suborbicular; apex 2–4-lobed by laciniiform to acuminate to occasionally subcaudate lobes of about equal size, the median lobes terminating in a uniseriate row of 2–5 cells, the median sinus descending to 0.15–0.35, the underleaf sinuses of subequal depth or, more often, the median sinus slightly to distinctly shallower and then the outermost processes appear apical-lateral or lateral in position (the underleaves then appear bifid), the apex and margins otherwise usually lacking other armature, the lobes or lamina margins sporadically with an accessory tooth.

Asexual reproduction absent.

Plants dioecious. Androecia seldom produced, subfolious, on main shoots or, less often, on leading lateral-intercalary branches, the androecia initially terminal but eventually becoming intercalary, short, with ca. 4 pairs of bracts per androecium. Bracts considerably smaller than leaves, the bracts often suberect to obliquely spreading, commonly dorsally assurgent in basal half, the distal half obliquely assurgent or more or less gently reflexed, the bracts loosely appressed to bract immediately above, the saccate portion fused toward base with opposite bract, the bracts with dorsal-basal portion distinctly ventricose and in profile with exposed walls of cells convex, the bract apices and margins as in vegetative leaves; lobule margin involute, with a several-celled tooth in distal sector and 1 or more sessile or stalked slime papillae; antheridia 1 per bract, large for bract size, the stalk short, 14–15 cells high, 2-seriate but with several local triseriate areas. Gynoecia on main shoot, long lateral-intercalary branches, and unfertilized subfloral innovations; subfloral innovations seen only associated with unfertilized gynoecia; vestigial stem perigynium present, the bracts and bracteoles of innermost series inserted on the vestigial perigynium. Bracts of innermost series much larger than leaves, erect and ensheathing perianth, free or connate

←

leaves, the other extending somewhat beyond them; note leaf lobe symmetry—some with subequal lobes, others with ventral lobe larger; dorsal view. The shoot also has an androecium terminal in position and a basal one that proliferates distally vegetatively, producing the sector shown (both androecia shown diagrammatically at right). **13.** ♂ Bract margin (dt = distal tooth). **14.** Plant with androecia on main shoot and on lateral-intercalary branches (dorsal view); note the spicate androecia (= sa, the basal one completely hidden by vegetative leaves), the terminal androecium on each of the 3 leading branches, and the intercalary androecium on the main shoot; note also that the branch at right has a basal androecium without subtending vegetative leaves, the branch then proliferates vegetatively distal to the androecium and ultimately produces a second androecium. (All from *Hatcher 505*, New Zealand, North Is., Waipoua Kauri Forest.)

dorsally, the median-basal portion concave, but the distal portion slightly to strongly convex (dorsal view), asymmetrically ovate; apices short bifid, the ventral lobe slightly to distinctly larger than the dorsal, the lobes entire; dorsal margin reflexed, often strongly so, entire; ventral margin reflexed, 1-dentate or entire. Bracteoles of innermost series somewhat smaller than bracts (ca. similar in width but shorter), connation variable: narrowly or broadly connate on both sides or broadly connate on 1 side and narrowly so on the other, concave (ventral view), ovate to broad elliptic; apices short bifid but occasionally divided to ca. 0.25, the lobes entire or with a few small teeth; lamina margins with 1(2) teeth or laciniiform processes in distal half, otherwise entire. Perianth moderately exserted beyond bracts, sharply trigonous throughout although sometimes slightly inflated, the perianth narrowly subobovate to less often oblong, not to moderately expanding toward the wide, rather deeply 3-lobed mouth, the lobes free for ca. 0.25–0.3 the perianth length; lobes shallowly but distinctly bifid, the segments narrowly acute to subacuminate, entire, the lobes otherwise coarsely dentate to small laciniate; keels sharp, the keelar wings common, exceptionally high, to ca. 0.5 the perianth width high and long decurrent on the vestigial perigynium, the free margin dentate to laciniate. Calyptra short, extending to ca. 0.5 the perianth length at maturity.

Seta 7–10 cells in diam., with 27–28 rows of outer cells surrounding a layer of cells in part of similar size, but the inner core cells much larger. Capsule elliptic, 1050 μm × 700 μm to 1260 μm × 735 μm, the wall 86–91 μm thick, of 6 (to locally 7) layers, the outer layer of cells equal to thickness of 1.6–2 of interior strata; outer layer of cells with a weak tendency toward two-phase development in some portions of valve, the cells subquadrate to short subrectangular, with red-brown nodular to short spine-like thickenings which are mostly on longitudinal walls and only sporadically on transverse walls, the longitudinal walls often with thickened continuous sheets of wall material, the exposed wall somewhat thickened; intermediate and inner layers subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended; inner layer of cells irregularly subquadrate to narrowly subrectangular, with semiannular bands common, wide, often nonpigmented in median portion, sometimes incomplete, often forking and anastomosing to delimit a series of well-delimited fenestrae.

Spores 12–15 μm, the wall thin, pale brown, with faint, dense, low but sharply defined close papillose and short-vermiculate markings; spore:elater diameter ratio 1.1–1.5:1. Elaters somewhat tortuous, mostly stout, often branched, 9.6–12 μm wide, 76–124 μm long, sporadically to 160 μm long, the spirals 2.9–3.4 μm wide, pale reddish brown.

Differentiation—The closest relative of *C. subopposítus* is *C. trialatus* of New Zealand, Tasmania, and mainland Australia, but *C. suboppositus* may be distinguished from that species by the shallowly divided underleaves, divided to at most 0.35; the dioecious condition; and the opaque and more rigid quality of the plants compared with the translucent, soft plants of *C. trialatus*.

Chiloscyphus suboppositus exhibits some affinities with *C. martianus* (Nees) J. J. Engel & R. M. Schust. of the Neotropics and with that species shares such features as the leaf apex asymmetry, with the ventral lobe considerably larger than the dorsal (Schuster, 1980, fig. 530: 8, 13, p. 234), the very high perianth keelar wings, and the deeply trilobed perianth with the lobes shallowly bifid. *Chiloscyphus suboppositus* differs from that species in the knot-like trigones, the dioecious condition, and the short, subfolious androecium.

Variation—There seems to be a correlation between presence of branch type and trigone size. Optimal plants have exclusively lateral-intercalary branching and distinct knot-like trigones. Suboptimal plants, on the other hand, may produce *Frullania*-type branching (but then only rarely and sporadically), and leaves of such shoots have medium-sized trigones (e.g., *Engel 14639*). This variant sometimes has leaves wider than in optimal plants (e.g., *Engel 14066*). Both conditions at times may be present in a single population, such as *Engel 14694*.

Another suboptimal phase of the species consists of smaller plants (2.4–2.5 mm wide) with wider leaves, several of which are subequally bilobed (intermixed with those having the more typical, distinctly asymmetric apices) and smaller underleaves with smaller armature. This phase occurs in subalpine scrub, and two collections are cited as examples: *Engel 20028* from Mt. Read (990–1010 m) and *Engel 19791* from below Black Bluff (1010 m). The subalpine plants may represent an extreme habitat or marginal ecological niche for the species. There should be no confusion of this phenotype with the quite different *C. edentatus*, which also is subalpine.

Oil-bodies of the Mt. Read plant (cited above) were studied and differ from the optimal phase in being 5–9(11) per cell, botryoidal, and on the whole a little larger, being 7.8–13 μm long × 4.6–5.9 μm wide, the orbicular ones being 6.5 μm. (The oil-bodies of the Mt. Read plant were subglobose to fusiform and often irregularly so.)

Note—The leaves are either free or weakly connate dorsally. Because this feature is sometimes difficult to observe with certainty, a series of shoot cross sections should be made. In such cases dorsal connation may be easily checked (Fig. 55: 8).

Distribution and Ecology—Limited to wetter sectors of Tasmania (sea level–1090 m) and one station in Victoria, Australia. The species is nearly exclusively associated with watercourses in cool valleys within rich, wet forests, such as *Nothofagus cunninghamii–Atherosperma–Eucalyptus–Eucryphia–Dacrydium franklinii* and others, or of *Eucalyptus–Banksia*. It occurs on sandy, gravely, or less often clayey soil of watercourse banks as well as on rocks and boulders associated with watercourses, particularly where some soil has accumulated. It is well represented in humid sites, such as near waterfalls and other wet niches. In upper elevation forests of *Nothofagus cunninghamii–Athrotaxis–Nothofagus gunnii* (e.g., 1040 m at Crater Lake, Cradle Mtn. area) the species sporadically occurs on the floor or on rocks at the edges of the lake.

Two collections were observed from the subalpine zone; both are suboptimal variants. One, from 990–1010 m on Mt. Read (*Engel 20028*), grew in a stream channel (but not submerged) in scrub consisting of *Richea scoparia*, *Nothofagus gunnii*, *Diselma*, and *Athrotaxis selaginoides*. The other collection, from 1090 m at Paddys Lake below Black Bluff (*Engel 19791*), occurred on the bank of a tarn, several inches above water level, in scrub of *Diselma archeri*, *Richea scoparia*, *R. sprengelioides*, dwarf *Nothofagus cunninghamii*, *Boronia citriodora*, and *Drimys lanceolata*.

Specimens Seen—**TASMANIA.** Along Arve Road about 1 mi. W of Willie Saddle, ca. 300 m, *Norris 29821* (F); Tahune Forest Reserve, off Pine Track, along Huon River, N of Hartz Mtn. Natl. Park, 70 m, *Engel 19945* (F); Mt. Wellington, Deep Creek, *Weymouth 494* as *L. bispinosa* (HO); track to Lake Judd, S of Mt. Eliza, E of Lake Pedder,

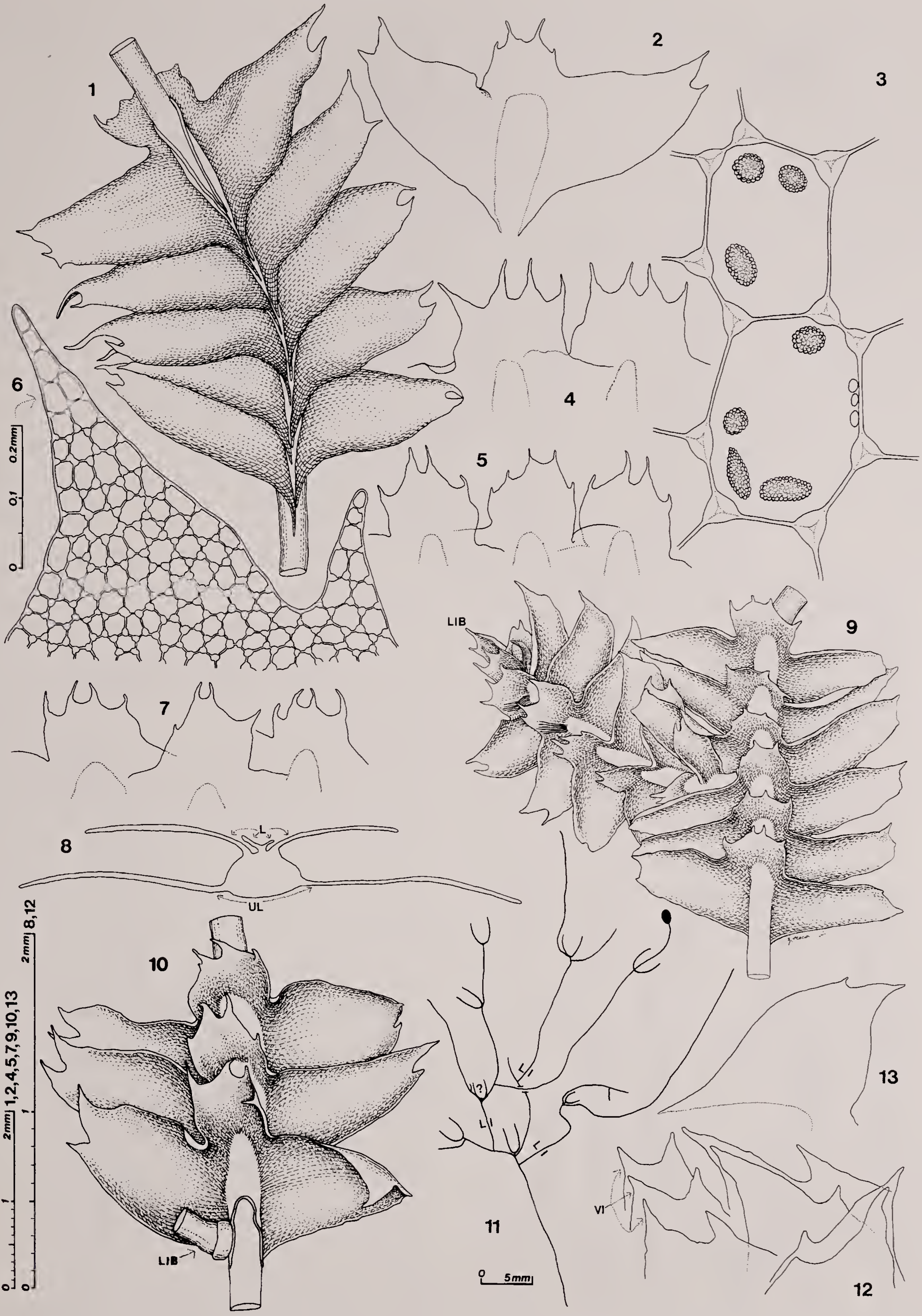

FIG. 55. *Chiloscyphus subopppositus* J. J. Engel. **1.** Portion of shoot, dorsal view. **2.** Opposing pair of leaves with attached underleaf (flattened). **3.** Oil-bodies, the lower cell also with chloroplasts (815×). **4, 5.** Underleaves. **6.** Distal portion of leaf. **7.** Underleaves (3). **8.** Cross section through shoot (l = leaf, ul = underleaf); note connation of innermost leaves. **9.** Portion of shoot, ventral view (LIB = lateral-intercalary branch). **10.** Portion of shoot, ventral view (LIB = lateral-intercalary branch). **11.** Cladograph, note repeated innovations from below perianth (LI = lateral-intercalary branch). **12.** Series of leaf apices to show variability (vl = ventral lobe, the ventral lobe otherwise is larger). **13.** Leaf. (**1, 2, 5–7, 9–13,** from type; **3,** from *Engel 19945*, Tasmania, Tahune Forest Preserve; **4,** from *Engel 14694*, Tasmania, Gordon River; **8,** from *Engel 14756*, Tasmania, Gordon River.)

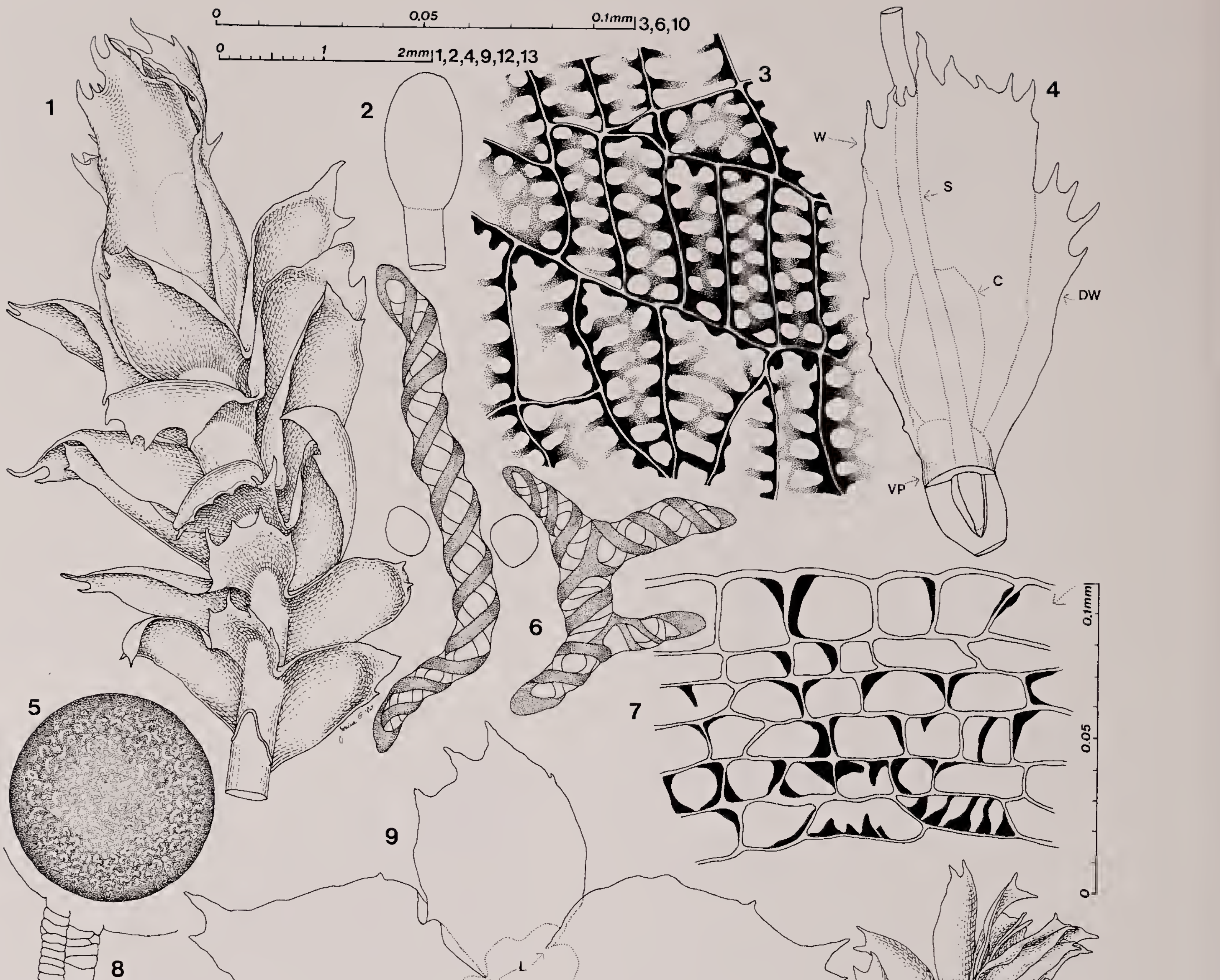

FIG. 56. *Chiloscyphus suboppositus* J. J. Engel. **1.** Gynoecium with enclosed sporophyte, ventral view. **2.** Capsule profile. **3.** Capsule wall, inner layer. **4.** Lateral face of perianth (dw = dorsal wing; w = wing; vp = vestigial perigynium, the base of which is shown in section; c = calyptra; s = seta). **5.** Spore (2210×). **6.** Unbranched and branched elaters and spore to same scale. **7.** Capsule wall, cross section. **8.** Antheridial stalk. **9.** ♀ Bracts and in middle, bracteole; note lamella (= L) on both connate sectors. **10.** Capsule wall, outer layer. **11.** Seta, cross section. **12.** Perianth mouth, ventral lobe in middle (note wings). **13.** Androecium-bearing shoot. (**1–7, 9–12,** from type; **8, 13,** from *Engel 19791*, Tasmania, Paddys Lake.)

520 m, *Engel 13765* (F); Gordon River, vicinity of Sir John Falls, just up river from Butler Is., ca. 50 m, *Engel 14756* (F); ibid., Sir John Falls, just up river from Butler Is., sea level, *Engel 14694* (F); ibid., Pine Landing, 6 mi. from river mouth and Macquarie Harbour, sea level, *Engel 14639* (F); ibid., Gorge Creek, near Pine Landing, sea level, *Engel 14668* (F); Griffiths Creek (tributary to Surprise River), ESE of Mt. Arrowsmith, 1.7 km via Lyell Highway W of King William Saddle and 17.4 km W of Derwent Bridge, 700–720 m, *Engel 19491* (F); Crotty Road [Kelly Basin Road], about 6 mi. S of Lyell Highway, *Norris 33487* (F); King River, 11.3 km by road from Regatta Point and 13.3 km by road from Strahan Harbour, stream which enters King River under wooden bridge, sea level, *Engel 14928* (F); Dubbilbarril, *Weymouth 1032* as *L. trialata* (HO); Dundas Creek, at bridge across Dundas Road, ca. 300 m, *Norris 31427* (F); ibid., near Concert Creek, ca. 400 m, *Norris 31369* (F); trail to Moore's Pimple, about 2 mi. E of end of Dundas Road, ca. 600 m, *Norris 31330* (F); Williamsford, *Weymouth 1037* as *L. trialata* (HO); ibid., near Mt. Read, ca. 305 m, *Weymouth 5943* as *L. trialata* (M); Mt. Read, S of Rosebery, 990–1010 m, *Engel 20028* (F); Murchison River at Murchison Highway, *Norris 33713* (F); Mt. Pelion E, 880 m, *Moscal s.n.* as *C. helmsianus* (F, HO); Cradle Mtn.–Lake St. Clair Natl. Park, Cradle Mtn. area, Weindorfers Forest, ca. 920–1080 m, *Jarman 88/11* (F); ibid., NE side of Crater Lake, 1040 m, *Engel 14066* (F); ibid., Pencil Pine Creek, just downstream from Knyvet Falls, road to Cradle Mtn., 780 m, *Rowlatt 37C, 38* (F); Paddys Lake, below and E of Black Bluff, SW of Nieta, 1090 m, *Engel 19791*–c. ♂ (F). **AUSTRALIA. VICTORIA:** Baw Baw Natl Park, western branch of West Tyers River, 1190 m, *Meagher & Scarlett 4351* (F).

Chiloscyphus trialatus (Gottsche) J. J. Engel & R. M. Schust.

Lophocolea trialata Gottsche, Linnaea 28: 552. 1856. *Chiloscyphus trialatus* (Gottsche) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 424. 1985 (1984). Type: "Australia, felix, Alpes australes," [*F. von Mueller*] (L!).

Lophocolea triangulifolia Steph., J. Linn. Soc., Bot. 29: 270. *p. 27, f. 11.* 1892, *syn. nov.* Type: New Zealand, North Is., *Colenso 983* (ex hb. Kew) (BM!, G!, WELT!).

Chiloscyphus pearsonii J. J. Engel & R. M. Schust., Nova Hedwigia 39: 421. 1985 (1984) (*syn. nov.*) *ut nom. nov. pro Lophocolea bicuspidata* Pearson, Bull. Misc. Inform. 1924: 71, *f. 1.* 1924, *nom. illeg., non L. bicuspidata* Steph., Spec. Hep. 6: 263. 1922 ≡ *Chiloscyphus bicuspidatus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 411. 1985 (1984) (Hawaii). Type: Tasmania, Mt. Wellington, Deep Creek Track, 1600 ft, 13 Nov. 1911, *Weymouth 1573* (BM!, HO![2]).

Chiloscyphus archeri J. J. Engel & R. M. Schust., Nova Hedwigia 39: 410. 1985 (1984), *ut nom. nov. pro Lophocolea tasmanica* Mitt. *in* Hooker f., Bot. Antarc. Voy. 3: 226, *pl. 178, f. 5.* 1859, *non Chiloscyphus tasmanicus* Steph., Bull. Herb. Boissier 8(2): 133. 1908 (= Spec. Hep. 3: 249). Type: Tasmania, *Archer* (BM!–c. per. + ♂; NY = *absens*, cf. Thiers, 1983, p. 291).

Plants soft and rather flexuous, delicate, loosely creeping to ascending, pale green to bright grass green, becoming darker green in deep shade, translucent, very nitid when dry; shoots medium, to 3.8 mm wide. Branches common, often copious, of *Frullania* type (the half-leaf deltoid and with the apex medium acute to apiculate) or lateral-intercalary type, the latter somewhat more common, sporadic populations with predominantly intercalary branching. Stems 13–14 cells high, the cortex moderately differentiated, in 1(2) layers of somewhat smaller cells, the cortical and medullary cells thin walled. Rhizoids in loose clusters from stem at immediate base of underleaves. Leaves opposite or nearly so, horizontal, widely spreading, loosely imbricate, weakly to distinctly connate dorsally or if free then the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf orientation and insertion strongly succubous, the insertion not recurved at ventral end, the leaf arrangement commonly covering much of stem in dorsal view except for narrow V-shaped sectors. Leaves broadly and at most moderately convex (dorsal view), asymmetrically ovate to subdeltoid, clearly widest near base, the dorsal-basal extremity dilated and forming a narrowly acute sector oriented toward shoot base; apex shallowly bifid, the lobes often detached, plane, usually unequal, the ventral larger than the dorsal, which is basal in juxtaposition to the ventral lobe, the lobes sporadically subequal; lobes acuminate (the dorsal sometimes narrowly acute, sometimes reduced to a mere small tooth), terminating in a uniseriate row of (1)2–3(4) slightly elongated cells, the lobe margins entire; dorsal margin ± straight, plane to abruptly and sharply deflexed, entire, decurrent; ventral margin gently and broadly rounded but sometimes with a moderate dilation in basal half, plane to slightly deflexed toward base, normally entire, very rarely with a tooth. Leaf cells with walls thin, trigones medium and straight sided to large and bulging (but relatively small in proportion to cell size), the median cells 25–40 µm wide, 34–53 µm long; surface faintly papillose. Oil-bodies hyaline, 6–7 to 10–12(14) per cell, coarsely botryoidal, the spherules protruding well beyond membrane, the oil-bodies typically elliptic, some spindle-like, others globose, most 11.8–13.7 × 5.9–7.8 µm, some 6.8–9.8 × 4.9–5.9 µm, the globose ones 5.9–8.8 µm in diam. Underleaves fragile, much smaller than leaves, *in situ* 1.8–2.4× stem width, rather broadly connate on both sides, the insertion often asymmetric, inverted U-shaped, the underleaves slightly spreading, approximate to contiguous, plane to moderately concave (ventral view), ± obtrapezoid to subquadrate; apex divided to 0.5–0.75 by a commonly broadly rounded to lunate sinus; lobes often partially or wholly detached, mostly diverging, sporadically ± parallel, acuminate to subcaudate, terminating in a uniseriate row of (1)2–4 cells, lobe margins entire or with a ciliiform process, the margin defining the sinus entire or 1–2-dentate-laciniate; lamina margins often recurved, particularly in vicinity of connation, with a laciniiform to lobiform process that is lateral or, if apical-lateral, then the outermost sinuses and median sinus sometimes subequal in depth and the underleaves appear 4-lobed; underleaf margins otherwise entire or with a tooth or cilium toward base.

Asexual reproduction absent.

Plants autoecious. Androecia of two basic kinds: 1) on main shoot or rather short to elongate indeterminate *Frullania*- or lateral-intercalary–type branches, the androecia subfolious, the bracts subfoliaceous, of similar basic shape as leaves but considerably smaller, the bracts ventricose at the base, the distal portion erect and vertical to widely spreading and subhorizontal, the bracts dorsally assurgent, the apex with lobe asymmetry as in leaves or the apex undivided, entire and narrowly rounded; and 2) on (often copious) short, abbreviated, lateral-intercalary branches that often are hidden or nearly so by lateral leaves above, the shorter ones appearing similar to the heteroscyphoid type, the androecia spicate to subspicate, the bracts much smaller than leaves, erect, vertical, dorsally assurgent, often strongly ventricose-subcucullate, so much so that the dorsal pocket is rather ill-defined and large in proportion to bract size, the apex undivided, entire, and truncate to narrowly rounded, occasionally bidentate. Lobule fused toward base with that of opposing bract, the free margin involute, with 2–4 few to several-celled teeth; antheridia solitary, the stalk biseriate. Gynoecia dorsally assurgent, on main shoot and short to long lateral-intercalary branches, the branches often without normal vegetative leaves, the gynoecia absent from *Frullania*-type branches; subfloral innovations absent; vestigial stem perigynium present, the bracts and bracteoles of innermost and second series inserted on the vestigial perigynium. Bracts of innermost series much larger than leaves, erect to obliquely spreading, often with at least the base appressed to perianth, weakly connate with each other, convex (especially distally) (dorsal view), narrowly ovate; apices short bifid, the ventral lobe slightly to distinctly larger than the dorsal or the lobes subequal, the lobe margins entire or occasionally with a tooth; lamina with dorsal margin reflexed, sometimes sharply so, entire or with 1–2 small teeth, the ventral margin broadly reflexed, entire or with to 4 small teeth. Bracteoles of innermost series somewhat smaller than bracts, connate on both sides, rather narrowly so on 1 side, moderately so on the other, concave (ventral view), narrowly ovate; apices bifid to at most 0.3, the lobes often with a few small teeth; lamina margins entire or with a few small teeth. Perianth longly exserted beyond bracts, trigonous and prismatic throughout, narrowly oblong, 5–6.7× longer than wide (not including wings) and of about equal width throughout, the mouth wide, deeply 3-lobed, the lobes free for 0.25–0.33 the perianth length; lobes narrowed distally, deeply bifid, the segments acuminate to (more often) caudate, sometimes with a tooth near the base, the lobes otherwise dentate to ciliate below level of segments; keels sharp, multicellular, with keelar wings common, exceptionally high, the height to ca. 0.5 the perianth width, decurrent on the vestigial perigynium, often undulate, the free margin dentate to subciliate. Calyptra small, extending to 0.25–0.35 the perianth length at maturity.

Sporophyte often emerging from a tear in the median sector of the perianth. Seta 7 cells in diam., with 29 rows of outer cells surrounding an inner core of scattered cells of similar size or slightly larger, the inner core, however, with 3–5 much larger cells which average 1.6× the diameter of other core cells, the inner core cells with corners thickened as in medium-sized trigones. Capsule long ellipsoid to cylindrical, 1120 × 595 μm to 1575 × 700 μm, 1.9–2.4× longer than wide, the wall 47–50 μm thick, of 5 (locally 6) layers; outer layer of cells equal to thickness of 1.8–2.5 of interior strata; outer layer of cells subquadrate to rectangular, the radial walls slightly and irregularly thickened, the walls with red-brown nodular to spine-like thickenings, the thickenings mostly on longitudinal walls and, less frequently or lacking on transverse walls, with semiannular bands sporadic, narrow and nonpigmented in median portion; intermediate layers each thicker than inner layer, the intermediate layers with vertical thickenings often considerably tangentially extended, sometimes becoming semiannular; innermost layer of cells irregularly quadrate to rectangular, the radial walls with moderately thickened sheets of wall material, with semiannular bands pale red brown, common, rather narrow, close and numerous, sometimes nonpigmented in median portion, sometimes incomplete, sometimes forked but then only sporadically anastomosing to delimit fenestrae, the radial walls with nodular thickenings rare.

Spores 9.6–11 μm, yellow brown, very thin, with faint, dense, low but sharply defined, close, papillose and short-vermiculate markings, spore:elater diameter ratio 0.85–1(1.1):1. Elaters tortuous, 9.6–11 μm wide, the spirals 2.4–3.4 μm wide.

DIFFERENTIATION—*Chiloscyphus trialatus* is the most specialized species in the section. For example, heteroscyphoid androecia are often present and copious; these are very small, easily overlooked, being nearly or totally hidden by the leaves above, and spicate (Fig. 58: 8). However, some variation exists among androecia restricted to abbreviated intercalary branches—androecial branches may be spicate and extend slightly beyond the apex of the leaf above or they may be, rarely, twice the leaf length and subspicate (Fig. 57: 7). The latter condition represents a step in reduction beyond the subspicate phases occasionally found among androecia on leading shoots. Androecia on main shoots or rather short to long terminal or intercalary branches are subfolious (Fig. 58: 8), chiloscyphoid in character and frequently produced (Fig. 57: 9, 10).

The range in gynoecial position is similar to that of the androecia—they are frequently heteroscyphoid in position and occur on abbreviated lateral-intercalary branches lacking normal leaves, or they may occur on leading shoots (Fig. 57: 10, 11). Unlike androecia, the gynoecia do not occur on terminal branches. Perianth shape, however, is distinctly chiloscyphoid in being prismatic throughout and narrowly oblong (Fig. 58: 6, 8), and unlike androecia, the perianth does not exhibit gradations toward the heteroscyphoid shape. The perianth shape, though, is specialized among *Chiloscyphus* taxa in being 5–6.7× longer than wide, very narrow throughout, and having exceptionally high wings (Fig. 58: 6, 8).

Other specialized features also occur in the species. The capsules are 1.9–2.4× longer than wide and at times linear, a shape rare in the family. Also, the spore:elater diameter ratio is among the lowest in the genus, being 0.85–1(1.1):1.

VARIATION—Heteroscyphoid androecia are common in some populations, as in *Engel 19157* (Fig. 58: 8), but are rare or apparently lacking in others. The presence of heteroscyphoid androecia is of taxonomic significance in Tasmania, since the two other species in the section occurring there lack them. Interestingly, all New Zealand species of sect. *Connati* at least at times produce heteroscyphoid androecia.

Careful search usually will reveal lateral-intercalary "buds" that consist of a collar of stem tissue sometimes accompanied by meristematic tissue (Fig. 57: 8). Such "buds" are variable in frequency—sometimes common to locally abundant, sometimes rare and sporadic. They are also variable in position with respect to shoot and sexuality and may occur on leading shoots with subfolious terminal or intercalary androecia, on shoots lacking subfolious androecia but bearing heteroscyphoid androecial branches, on sterile shoots, as well as on leading gynoecium-bearing shoots. Normally branch growth does not occur beyond the "bud" stage, but in a few cases very short axes occur on which one young male bract is discernable (e.g., in *Schuster 67-3250*). The "buds" may indeed be androecial, but a firm connection between the "bud" and young branch stages has not been made. If the "buds" are eventually found to be androecial, then one may postulate a dormancy factor wherein androecial branches are "held" in a "bud" stage prior to possible subsequent elongation into functionally male branches.

The dorsal-basal extremity of the leaf is dilated and forms a sharply and narrowly angular sector that is oriented toward the shoot base (Fig. 57: 7). The leaves often are connate dorsally, but the form of connation is variable. Connation may be symmetrical and involve the dorsal-basal extremities of both opposing leaves and then sometimes form a weak trough. However, the connation is often asymmetrical and involves attachment of the dorsal-basal extremity of a leaf with the lamina base of the opposing leaf at a site somewhat removed from the dorsal-basal tip (Fig. 57: 1). Here one leaf is somewhat more basal than the opposing leaf, and the sector

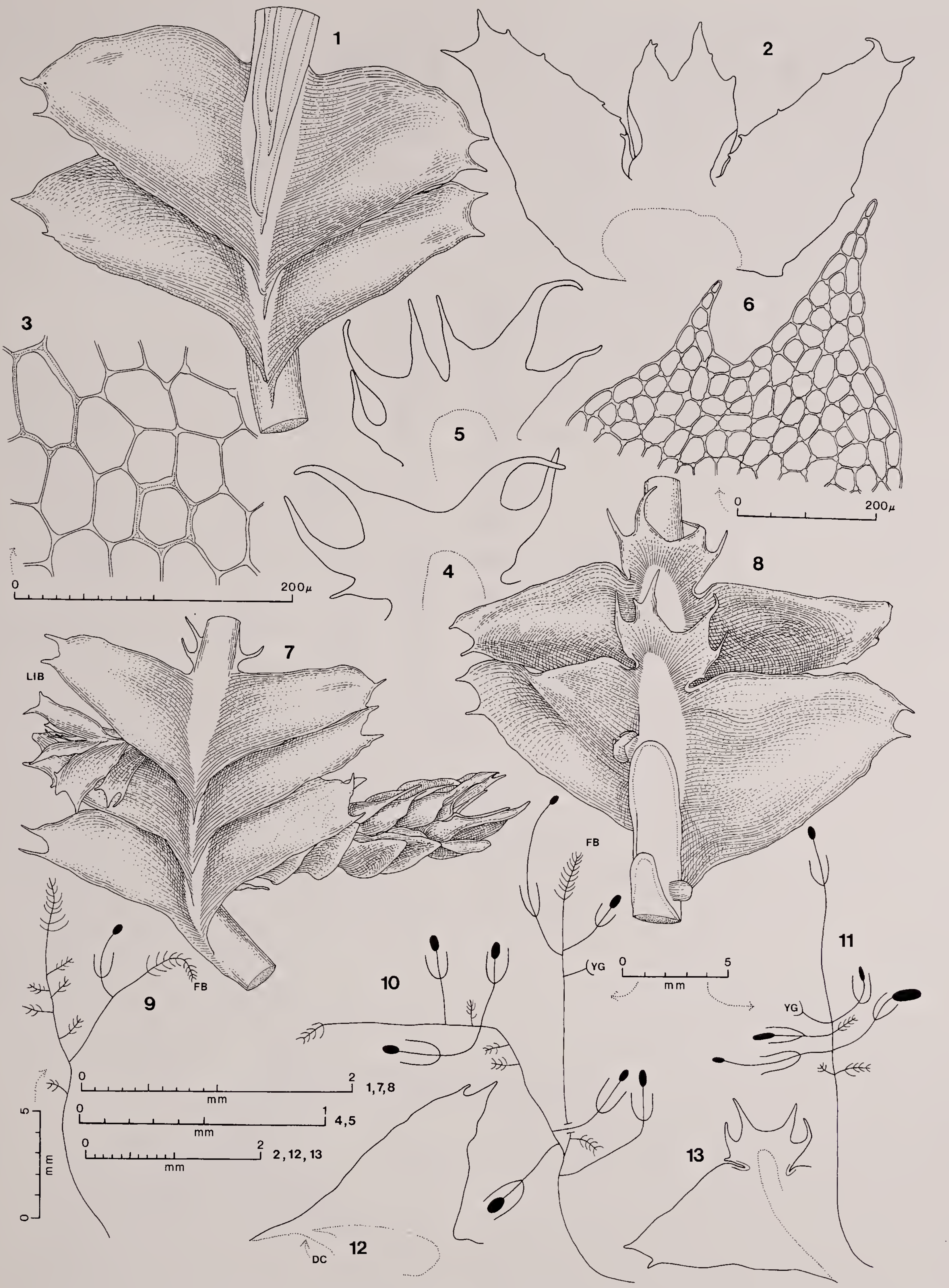

FIG. 57. *Chiloscyphus trialatus* (Gottsche) J. J. Engel & R. M. Schust. **1.** Sector of shoot, dorsal view; note dorsal connation of leaves. **2.** ♀ Bracts and in middle, bracteole. **3.** Median leaf cells; note dimorphism of cells and trigone magnitude. **4, 5.** Underleaves. **6.** Leaf apex. **7.** Androecium on lateral-intercalary branch of ca. 2× length of leaf above; note sterile lateral-intercalary branch (= lib) at left. **8.** Sector of shoot, ventral view; note "buds" at left and right of underleaf insertions, the latter not yet with a collar. **9–11.** Cladographs; all branching is lateral-intercalary except where indicated (FB = *Frullania*-type branch; U-shaped symbols indicate perianths, the stalked solid oval a sporophyte; yg = young gynoecium). **12.** Leaf outline (dc = dorsal connation). **13.** Leaf and attached underleaf. (All figures from *Engel 19157*, New Zealand, South Is., Paparoa Range.)

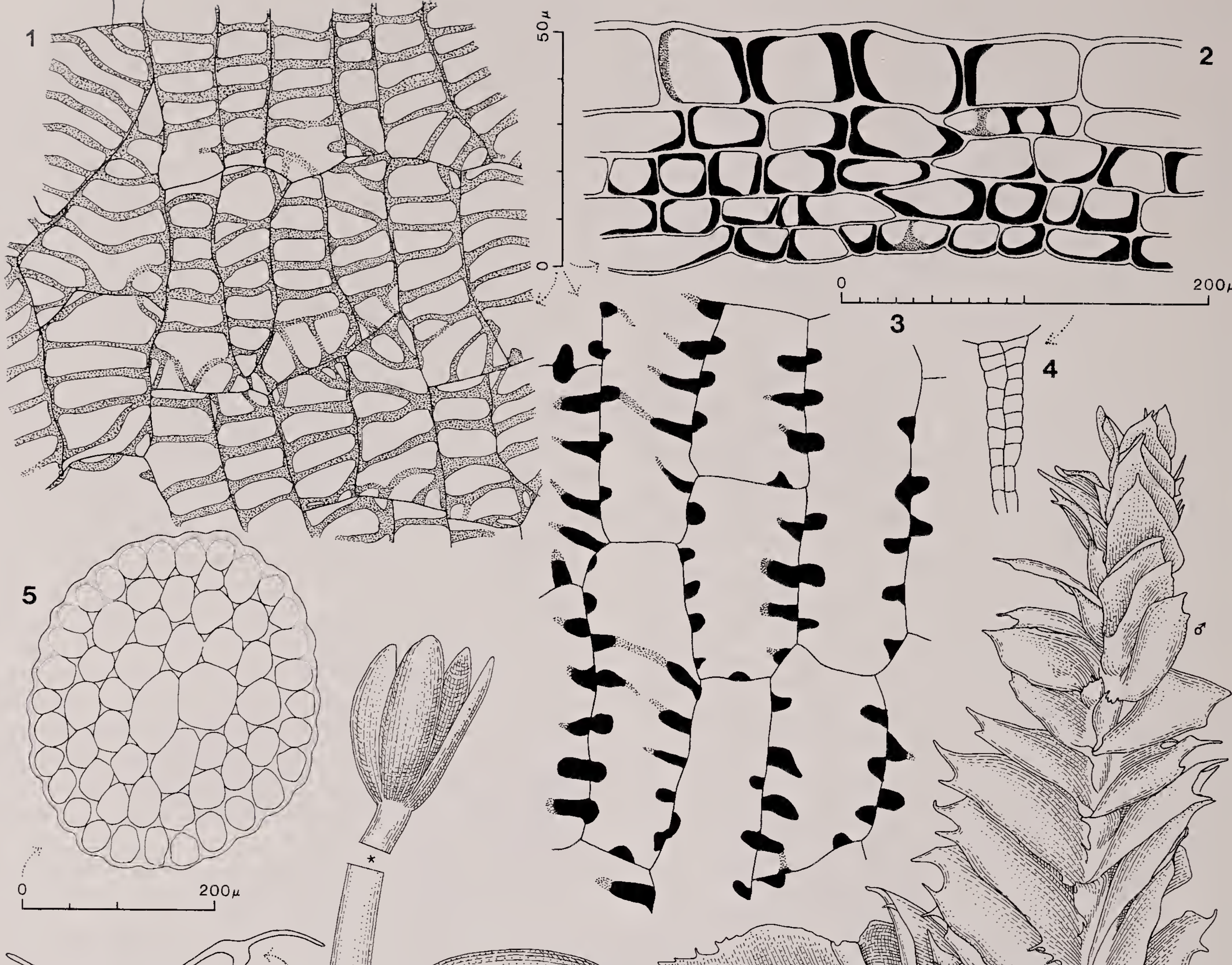

FIG. 58. *Chiloscyphus trialatus* (Gottsche) J. J. Engel & R. M. Schust. **1.** Capsule wall, inner layer. **2.** Capsule wall, cross section. **3.** Capsule wall, outer layer. **4.** Antheridium. **5.** Seta, cross section. **6.** Perianth, cross section; note large wing on each keel. **7.** Distal sector of perianth, ventral lobe in middle (wings not shown). **8.** Shoot with 2 mature sporophytes (note long, narrow perianths with conspicuous, high, keelar wings), very young gynoecium (= ♀), and androecia terminal on main shoot as well as on abbreviated lateral-intercalary branches (noted by ♂ symbol in lower sector of figure). (All figures from *Engel 19157*, New Zealand, South Is., Paparoa Range.)

basal to the connation is decurrent. The leaves also may be free dorsally.

Underleaf lobes usually are widely divergent, with an intervening lunate sinus. The underleaves, however, sporadically have lobes ± parallel and with the intervening sinus narrowly rounded. The latter condition tends to occur in the vicinity of androecia.

Frullania-type vegetative and sexual branches usually are frequent and provide a useful distinction from *C. multipennus*. However, sporadic populations, such as *Hatch s.n.* (CHR), have exclusively lateral-intercalary branching. In such populations one must rely on other distinguishing characteristics, such as dorsal connation, plant translucency, monoecious inflorescence, etc.

NOTE—1) Stephani did not have a concept of *L. trialata* as evidenced by a suite of specimens at HO determined by him. Stephani misapplied that name to specimens that actually belong to the following species in addition to *C. trialatus*: *C. suboppositus*, *C. semiteres*, *C.* sp. (sect. *Lophocolea*), *Heteroscyphus coalitus*, and *Leptoscyphus* sp.

2) Plants have an odor, without being crushed, similar to that of *C. helmsianus* but much less pungent. Notable also is that the two species belong to the same section.

NOTES ON TYPE SPECIMENS—1) *Lophocolea trialata* Gottsche. After considerable search I was able to locate only a single small collection of what I believe to be type material. The collection, at Leiden, bears scanty label data—7. *Lophocolea trialata*, Australia felix, Alpes australes, "herb. Lundg. Bot."[7]

The specimen lacks collector name, but the plants agree closely with the protologue (which contains locality/collector data only in the title of the paper—"Hepaticae Australasiae a Dre. Ferd. Müller lectae" [Gottsche, 1856, p. 547]). Type material is lacking at BM, BR, C, E, FH, G, GOET, H, HBG, M, MANCH, MEL, NSW, NY, PC, S, and W.

The rather flaccid plants have asymmetrically bifid leaves, the ventral lobe being notably larger than the dorsal. Leaf margins are usually entire, but the ventral may have, though rarely, a tooth as indicated in the protologue. Underleaves are broadly connate on both sides and are bifid to ca. 0.6–0.8, and lamina margins on each side have a small to large laciniiform process. Plants are monoecious; gynoecia are on short lateral-intercalary branches, and androecia are on short to rather long branches of the same type. Perianths are in rather poor condition but important details are discernable: lobes are deeply bifid by acuminate to subcaudate segments, and keels have well-developed wings. I observed only lateral-intercalary branches.

2) *Lophocolea bicuspidata* Pearson. The plants are flaccid, which accounts for the minute trigones. Several shoots show the monoecious condition. Perianths are mostly young and still included within the bracts or slightly exserted; elongate ones are rare, and these are typical of the species.

3) *Lophocolea tasmanica* Mitt. The specimen consists of delicate, markedly translucent shoots. Underleaves are ca. 0.6–0.8-fid and on each side have a ciliiform to laciniiform process. The asymmetrically bifid leaves are dilated at the dorsal base and decurrent on the stem. I was able to establish sexuality on several shoots, all being monoecious. On two shoots the androecium is terminal on the main shoot and the gynoecium occurs on a short, lateral-intercalary branch lacking normal leaves. Another shoot has an androecium on a (?)*Frullania*-type branch and several gynoecia on abbreviated, lateral-intercalary branches, one perianth being elongate, prismatic and with very high wings.

4) *Lophocolea triangulifolia* Steph. I have studied original material of this species from several herbaria, each specimen consisting of only a few shoots. The specimen at G serves as an example: it consists of 4–6 soft, lax, flaccid, delicate, pale, translucent shoots. Leaves are often connate dorsally and bifid (the ventral lobe much larger than the dorsal), and leaf cells have small trigones as would be expected from a flaccid plant. Underleaves are distinctly connate with leaves on both sides and divided nearly to the base, the lamina being of ca. 4 cells high. Terminal branching is present: the G specimen has two branches, one lateral intercalary, the other of the *Frullania* type; two shoots were studied from the BM specimen—one has one *Frullania*-type branch, the other shoot has three terminal branches (intercalary branches are lacking); the WELT specimen consists of two shoots, and of the 7 branches present on these shoots, 6 are terminal.

Despite the completely sterile condition of the original material, the translucent appearance, the presence of terminal branching, and the often dorsally connate leaves dictate placement of the species with *C. trialatus*. Hodgson (1953) placed the species in the synonymy of *Lophocolea pallida* (= *C. multipennus*).

DISTRIBUTION AND ECOLOGY—Known from New Zealand (South Is., 10–170 m; North Is., sea level–1100 m), Chatham Is.; Australia: Tasmania (180–500 m), Victoria, New South Wales (960 m).

Throughout its range the species occurs in rich forests, particularly those with a tree fern component, and it grows for the most part in well-drained niches. It frequently grows epiphytically on tree fern trunks (e.g., *Cyathea medullaris* in New Zealand), and even after the fall of the tree fern, the species may persist over its decaying remains on the forest floor. The species also occurs on shaded, wet, rotted, bryophyte-covered logs and stumps, as well as over wood that is in advanced stages of decay on the forest floor. For example, at Omaha (North Auckland Prov., New Zealand, *Engel 20370*), it grows over rotted duff of *Gahnia* in a swampy forest dominated by *Vitex*, *Freycinetia*, and *Gahnia xanthocarpa*. At Kaimai-Mamaku Forest Park (North–South Track accessed from Old Kaimai Road), plants occurred over humus debris under cover of *Blechnum* fronds under the lip of a bank at the margin of a forest of *Weinmannia racemosa* with occasional emergent *Dacrydium cupressinum*. It exceptionally occurs on tree bark some distance above the floor. The species occasionally occurs on soil or over stones or exposed roots.

The species has an interesting distribution in New Zealand. It is sporadic on South Is., with relatively few known stations in the southern half of the island (it is unknown from Otago Prov. and is known from a single station in Westland Prov.). Also, on South Is., the species apparently is absent in forests above 170 m. On the other hand, the species is quite common on North Is., where it ranges from Wellington Prov. to Radar Bush near Cape Reinga. It is particularly common in South Auckland and North Auckland Provinces. Compared with South Is., the species has a much broader altitudinal range; it occurs from sea level to 1100 m on North Is.

In Tasmania the species appears to be confined to the drier, eastern half of the island. It is sporadically distributed between 180 and 500 m.

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[7] "Australia felix" has been used to designate the fertile district of central Victoria.

This appears to be a warm-temperate species that flourishes in forests that are warmer and receive moderate but not heavy amounts of rainfall.

Specimens Seen (selected)—**NEW ZEALAND.** Without specific loc., *Knight s.n.* as *L. tasmanica* (M). **STEWART ISLAND:** Port Pegasus, sea level-ca. 45 m, *Engel, von Konrat & Braggins 24271* (F). **SOUTH ISLAND. SOUTHLAND:** Lake Hauroko, ca. 120 m, *Child H 1603* as *L. multipenna* (F); Fiordland Natl. Park, Milford Track, track between boat landing at Arthur River and Sandfly Point, Milford Sound, *O. Schuster 103*–c. sporo. (F); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18830* (F). **WESTLAND:** Fox Glacier, on trail to Cone Rock, *Schuster 67-3250*–c. sporo. (F). **NELSON/WESTLAND PROV. BOUNDARY:** Paparoa Range, S side of Porarari River in limestone gorge, E of Punakaiki, 10 m, *Engel 19157*–c. sporo. (F); same loc., ca. 30 m, *Fife 4933* (F); gorge of the Porarari River, true left bank, 0.5–3 km above Rte. 6 bridge, less than 30 m, *Fife 6096* (F). **NELSON:** Paparoa Natl. Park, Bullock Creek Road, along Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel 21611*–c. sporo. + ♂ (F); Paparoa Range, upper slopes of N side of Tiropahi or Four Mile River between sea and Rte. 6, S of Charleston, 130–170 m, *Engel 19259*–c. sporo. (F). **NORTH ISLAND. WELLINGTON:** Taurewa, *Braggins H16* (AK); Tongariro Natl. Park, ca. 7 km from Ohakune on Ohakune Mtn. Road, 900 m, *Engel 22707*–c. per. + ♂ (F). **GISBORNE PROV.:** Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20587*–c. per. + ♂ (F). **NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY:** Urewera Natl. Park, crest trail from Highway 38 toward Whakataka summit, N of northern extremity of Lake Waikaremoana, 930–1030 m, *Engel 20631*–c. per. + ♂ (F); ibid., track from NS road to Mt. Whakataka, the Whakataka track, 945–1100 m, *Schuster 67-1605* (F). **SOUTH AUCKLAND:** Puaiti Bush, S of Rotorua, *Allison H 543* as *L. multipenna* (CHR); Pureora State Forest Park, Waipapa Ecological Area, *Braggins et al. 144b* (AK); Mamaku Plateau, W of Lake Rotorua on Rt. 5, 400 m, *Engel 20505*–c. per. + ♂ (F); above Murupara, Rotorua Region, *Allison H 599* as *L. multipenna* (CHR); Ngongotaha Mtn., Rotorua, *Allison H 3643* as *L. pallida* (CHR); between Lake Rotoehu and the coast, Bay of Plenty, *Allison H 3644* as *L. pallida*–c. sporo., *H 3645* as *L. multipenna*–c. sporo. (CHR); Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel 22120*–c. per. + ♂. (F); Kaimai-Mamaku Forest Park, North–South Track accessed from Old Kaimai Road, 480–520 m, *Engel & von Konrat 27570* (F); Coromandel Peninsula, Kauri Clump Forest Reserve, W side of Peninsula, 185–245 m, *Schuster 67-3672A* (F). **NORTH AUCKLAND:** Nihotapu Valley, Auckland, 150 m, *Hatch s.n.* as *L. pallida* (CHR); Titirangi, Auckland, *Ashcroft L 12* as *L. pallida*–c. sporo. (CHR); NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel 20424* (F); ibid., Spraggs Bush, ca. 360 m, *Engel 22196*–c. young ♀ + ♂ (F); Pohuehue Scenic Reserve, N of Auckland on State Highway 1, ca. 25 m, *Engel 21167*–c. per. + ♂ (F); Omaha, just E of causeway to Omaha Beach, 2 m, *Engel 20370*–c. per. + ♂ (F); summit of ridge W of Bream Head, SE of Whangarei, 425 m, *Engel 22269*–c. per. + ♂ (F); Waipoua Kauri Forest Preserve, Big Tree Kauri area, *Schuster 67-3808* (F); Waipoua Forest, *Allison H 747* as *L. pallida*–c. sporo. (CHR); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21104*–c. sporo. (F); Waima Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, off Waiotemarama Track, 650–680 m, *Engel 22624*–c. young & + ♂ (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel 21010*–c. per. + ♂ (F); Mangamuka Gorge Reserve, N of crest, SE of Kaitaia, NW of Mangamuka, ca. 305 m, *Schuster 67-1077* (F); Radar Bush, WSW of Cape Reinga, S of Mt. Te Paki, ca. 100 m, *Engel 20856*–c. per. + ♂ (F). **Chatham Is.:** Southern Tablelands, Te Mangahou Creek, 40 m, *de Lange CH 1988* (AK, F). **TASMANIA.** E side of Tasman Peninsula, E facing slope of Tatnells Hill, S of Waterfall Bay, 500 m, *Engel 13126* (F); St. Marys Pass, The Glen, 275 m, *Weymouth 1342, 1343* as *L. multipenna* (HO); Franklin-Arve Rivulet, *Weymouth s.n.* (HO); Mt. Wellington, Deep Creek Track, *Weymouth 1008* (HO); ibid., Deep Creek, *Weymouth 97* (HO); ibid., Lady Edeline Falls, 185 m, *Weymouth 1180* (HO); ibid., Hobart Rivulet, *Weymouth 454* (HO); ibid., Guy Fawkes Rivulet, *Rodway s.n.* (HO); Mt. Field, Russell Falls, *Rodway s.n.* (HO); Notley Gorge, 180–280 m, *Rowlatt 73* (F). **AUSTRALIA. VICTORIA:** Pioneer Creek Road, which leads S from road between Powelltown and Noojee, *Engel 16852*–c. sporo. (F); Great Dividing Range, Maroondah Highway just NE of Fernshaw and NE of Healesville, *Engel 16805*–c. per. + ♂ (F). **NEW SOUTH WALES:** Monga, 20 km SE of Braidwood, 960 m, *Curnow & Streimann 641*–c. sporo. (NY); Lawson, *Watts 665* (NSW); Blackheath, Rodriguez Pass, *Watts 1002* (NSW).

Chiloscyphus edentatus J. J. Engel

Chiloscyphus edentatus J. J. Engel, Phytologia 83: 43. 1998 (1997). Holotype: Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park, Ballroom Forest, SW side of Lake Dove, 950–1050 m, *Engel 13993* (F); isotype: (HO).

Plants with the superficial appearance of *C. austrigenus* in dorsal view and *C. leucophyllus* in ventral view, soft and rather flexuous, brittle, light green, darker toward base; shoots to 2.2 mm wide. Branches frequent, predominantly to exclusively terminal and of *Frullania* type (the half-leaf with same basic shape as vegetative leaves, but the apex undivided and acuminate or less often apiculate), the branches sporadically of lateral-intercalary type. Stems 9–10 cells high, the cortex rather well differentiated, in 1–2 layers of smaller cells with somewhat thickened walls, the cells of the outermost layer clearly the smallest, the cells of the penultimate row often somewhat larger but distinctly smaller than central medullary cells. Rhizoids sparsely developed, in tight fascicles from stem at immediate base of underleaves. Leaves subopposite, vertical to subvertical, the adaxial faces of opposing leaves often closely juxtaposed or touching, the leaves strongly dorsally assurgent, mostly erect to suberect, less often obliquely spreading, loosely imbricate, free dorsally, the orientation subtransverse to subsuccubous, the insertion strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement allowing for exposure of rather wide sectors of the stem in dorsal view. Leaves convex (dorsal view), especially so distally, in ventral view often appearing canaliculate near apex, the leaves asymmetrically broad ovate to subdeltoid, clearly widest near base, the ventral-basal portion of leaf dilated and the ventral margin thus broadly rounded to subauriculate toward the base, the margin descending well below stem prior to becoming connate with underleaf, the leaf subsequently abruptly narrowing distally, the ventral margin often forming an "S" or reversed "S" configuration (depending on side of stem); apex variable: undivided, narrowly rounded, and entire to retuse to very shallowly bilobed, the lobes then subequal or, often, the ventral lobe larger than the dorsal, which is sometimes somewhat basal in juxtaposition to the ventral lobe; lobes (when present) narrow to medium acute to subacuminate, sometimes apiculate, the ventral terminating in a uniseriate row of 2–4(5) isodiametric cells, the tip cell slightly longer than wide; dorsal segment grading from a large tooth (and subequal to the ventral) to a small tooth to a low rounded projection to absent altogether; lobe margins entire; dorsal margin ± straight in basal sector, but broadly and gently rounded distally, broadly and gently deflexed, entire, very long decurrent; ventral margin often somewhat undulate, broadly and gently deflexed (especially the dilated portion) or plane, the alignment variable: apical ventral to ventral, or if margin reflexed, then ventral-basal, the margin entire. Leaf cells smooth, without protuberances of any sort, with walls thin, trigones medium to knot-like, rarely and sporadically small and concave sided, median leaf cells 28–34 μm wide, 24–34 μm long. Oil-bodies large for cell size yet occupying only fraction of lumen volume, 2(3, very rarely 5) per cell, botryoidal, broadly to narrowly elliptic to long linear, often

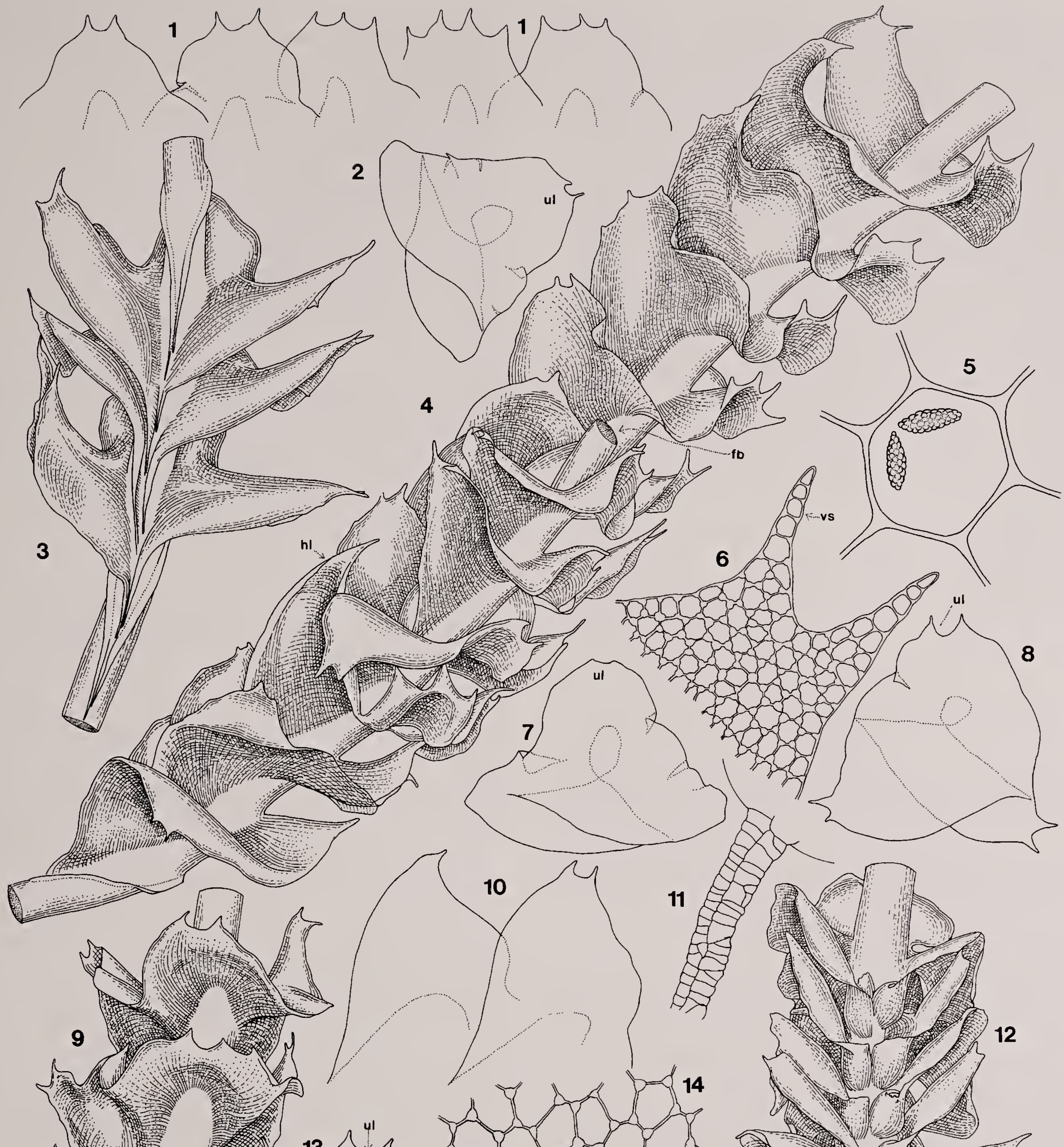

FIG. 59. *Chiloscyphus edentatus* J. J. Engel. **1.** Series of five underleaves. **2, 7, 8, 13.** Opposing leaf pairs with underleaves (= ul). **3.** Portion of shoot, dorsal view. **4.** Lateral view of shoot with *Frullania*-type branch (= FB; HL = half-leaf). **5.** Median leaf cell with oil-bodies (note exceptionally small trigones) (1635×). **6.** Distal portion of leaf (VS = ventral segment). **9.** Portion of shoot, ventral view. **10.** Leaves (note difference in leaf apices). **11.** Antheridium. **12.** Portion of shoot with androecium. **14.** Median leaf cells. (**1, 3, 4, 6, 8–10, 13, 14,** from holotype; **2, 5, 7,** from *Engel 19656*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park; **11, 12,** from *Engel 13989*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park.)

irregular in shape and then subtriangular in profile or crescentic, 8.5–11.1 × 3.9–5.9 μm to 12.4–13 × 4.6–5.9 μm. Underleaves much smaller than leaves, *in situ* (2.2–)2.4–3.6× stem width, very broadly connate on both sides, the insertion inverted U-shaped, the underleaves strongly spreading, contiguous to loosely imbricate, concave, particularly toward the base (ventral view), the margins reflexed but the apex either oriented toward shoot apex, or, if reflexed, then the underleaves ± cucullate; flattened leaf and underleaf margins ± imperceptibly merging and with at most a slight angulation at the site of the connation, the underleaf lamina forming a hemispherical bulge (the lamina subquadrate in 4-lobed underleaves); apex retuse-bidentate to 2(3, rarely 4)-lobed to 0.3 by entire segments that grade from apiculate to cuspidate to subacuminate and that terminate in a unicellular row of 2–4 cells, the sinus narrowly rounded to lunate, if 2 or 3 sinuses present, then of subequal depth or the median sinus a little shallower, the apex and margins otherwise entire, the lamina margins sporadically with a sharp or rounded, shoulder-like projection distally.

Asexual reproduction absent.

Plants apparently dioecious. Androecial shoots ± isophyllous, the androecia subfolious, on main shoots or, less often, elongate *Frullania*-type branches, the androecia initially terminal but eventually become intercalary, rather long, and with 8–13 pairs of bracts per androecium. Bracts much like leaves in shape and form except for 1) the somewhat smaller size, 2) the transverse orientation, and 3) the development of a small lobule; bracts loosely imbricate, the saccate portion distinctly fused toward base with opposite bract, the bracts with dorsal-basal portion distinctly ventricose and in profile with exposed walls of cells convex; lobule small for bract size, margin involute, crenulate and with several sessile or stalked slime papillae (the stalk unicellular); antheridia solitary, rather small for bract size, the stalk 20–23 cells long, biseriate but with several local triseriate areas. Gynoecia not seen.

DIFFERENTIATION—This species has a striking yet superficial appearance to *C. leucophyllus* but differs from that species and all other *Leucophylli* by possessing uniformly smooth leaf cells. It may be further distinguished from *C. leucophyllus* by 1) the subvertical to vertical leaf orientation (Fig. 59: 4); 2) the polymorphic, often undivided and narrowly rounded to retuse leaf apices (Fig. 59: 2, 7); 3) the uniseriate row of the ventral leaf segment consisting of 2–4(5) cells (Fig. 59: 6); and 4) the uniformly entire leaf and underleaf margins (Fig. 59: 2, 7, 8). The species is a rather specialized element of sect. *Connati*.

The nearest ally to *C. edentatus* appears to be *C. suboppositus*. The two species may be distinguished by characters in the key.

VARIATION—The leaf and underleaf apices are quite variable. Some populations, such as the type, are predominantly symmetrically to asymmetrically very shallowly bilobed (Fig. 59: 6, 9, 13). Such plants also have predominantly short-bifid underleaves with a distinct, rounded to lunate sinus (Fig. 59: 1, 9). Other populations, such as *Engel 19656*, have leaf apices frequently undivided and narrowly rounded, and only occasionally 1- or 2-toothed (Fig. 59: 2, 7). Moreover, plants such *Engel 19656* have underleaf apices predominantly retuse-bidentate and only sporadically short bifid (Fig. 59: 2, 7). However, these correlations are not always consistent. For example, plants of *Engel 13964* have leaf apices mostly without teeth, but the underleaves are often short bifid.

Branching is predominantly to exclusively terminal and of the *Frullania* type. Some populations, such as *Engel 13993* and *14109*, have exclusively *Frullania*-type branches, and even after lengthy searches, intercalary branches were not found. However, occasional populations, such as *Engel 13964*, have lateral-intercalary branches in addition to terminal branches.

DISTRIBUTION AND ECOLOGY—A narrowly endemic species known only from higher elevation watercourses in the Cradle Mtn. area of Tasmania. It occurs over rock of stream beds in *Nothofagus–Athrotaxis* forests (950–1050 m), sometimes forming immense populations. In subalpine–alpine areas, it occurs at 1250 m on creek banks, the lower parts of the population often at water level, and on peaty soil on the lips of small rivulets.

SPECIMENS SEEN—**TASMANIA.** Cradle Mtn.–Lake St. Clair Natl. Park, Marigold Creek, W of and draining into Crater Lake, vicinity of Crater Peak Lookout, 1250 m, *Engel 14109* (F); ibid., Ballroom Forest, SW side of Lake Dove, 950–1050 m, *Engel 13989*–c. ♂ (F); ibid., Plateau Creek area, between Cradle Plateau and Marions Lookout, NNW of Cradle Mtn., 1250 m, *Engel 13964*, *13976* (F); ibid., Cradle Mtn. area, Plateau Creek, between Overland Track and Kitchen Hut Track, W of N end of Lake Dove, 1250 m, *Engel 19656* (F).

Sect. *Leucophylli* J. J. Engel

Chiloscyphus sect. *Leucophylli* J. J. Engel, Bryologist 94: 312. 1991. Type: *Jungermannia leucophylla* Hook. f. & Taylor

Leaf, underleaf (exc. *C. connatifolius*), and perianth cells armed on both surfaces with a single prominent, central, solitary, dome-like, thick-walled tuberculae (the tuberculae obscure or appearing absent in *C. aculeatus*). Underleaves distinctly connate on both sides. Plants dioecious.

The *Leucophylli* are restricted to Australasia; all taxa in the section are treated here.

Interesting inter-relationships and trends occur among the *Leucophylli* taxa. *Chiloscyphus tuberculatus* is the least specialized species, and provides clues to trends within the section. In *C. tuberculatus*, for example, underleaves are deeply divided into 2 or 4 lobes (Fig. 60: 10). The *Leucophylli* otherwise have undivided underleaves with a pair of well-developed laciniiform processes at the juncture of the margin and apex, while the intervening sector of the apex has smaller armature grading from dentate-ciliate in *C. leucophyllus* (Fig. 65: 8) to copiously spinose dentate-laciniate in *C. mittenianus* (Fig. 69: 8). *Chiloscyphus tuberculatus* has preserved leaf symmetry more than any other member of the *Leucophylli*. In this species the two lobes are of ± equal magnitude and without tendency for the dorsal lobe to become smaller and basal in juxtaposition to the ventral (Fig. 60: 10). *Chiloscyphus leucophyllus* is more specialized in having weakly asymmetrically bifid leaves, with the ventral lobe at most moderately larger than the dorsal, and the dorsal lobe at times basal in juxtaposition to the ventral (Fig. 65: 13). The extreme occurs in *C. mittenianus*, where we find strongly asymmetrically bifid leaves, with the ventral lobe much larger than the dorsal, which is distinctly basal in juxtaposition to the ventral lobe (Fig. 69: 5, 8). Differences in leaf symmetry are linked with the degree of dilation of the ventral-basal portion of the leaf. At most, moderate dilation occurs in *C. tuberculatus* and *C. leucophyllus*, but distinct and well-developed dilation is exhibited in *C. mittenianus* (compare Figs. 60: 10 and 65: 13 with Fig. 69: 5).

Interesting differences in reproductive structures occur among the species in the section. If one assumes that the least specialized ♂ bract lobules are those that are leaf-like, and those that show greater differentiation from leaves are more specialized, then some interesting trends emerge in the *Leucophylli*. *Chiloscyphus tuberculatus* is again the least specialized: it retains teeth on the lobule margin as well as conspicuous tuberculae of lobule surface cells (Fig. 60: 6, 7). Both of these features have been lost in *C. leucophyllus* and *C. mittenianus*—the lobule margins are crenulate, whereas lobule surface cells are smooth. The perianth also provides clues. The ability to produce bifid perianth lobes occurs in *C. tuberculatus* (Fig. 61: 2), although the character is not always expressed or obvious. The other species of *Leucophylli* have lost the ability and have undivided lobes (Figs. 66: 7; 70: 10).

Chiloscyphus tuberculatus is also a critical species in that it provides a connecting link to sect. *Lophocolea* and at the same time is a pivotal species in assessment of the origin of the *Leucophylli*. The counterpart of *C. tuberculatus* in sect. *Chiloscyphus* seems to be *C. bispinosus*. The two species have leaves deeply bifid by caudate to piliferous lobes, with the leaf lamina and lobes bordered by a row of enlarged cells, and deeply divided underleaves. Although the two species have a strikingly similar facies, plants of *C. tuberculatus* immediately may be separated by the tuberculate leaf cells, the more shallowly divided underleaves (median sinus descending to 0.4–0.5) that are distinctly connate on both sides, and the ciliiform projections on the ventral margin of the leaf. *Chiloscyphus bispinosus* has smooth leaf cells, underleaves divided to 0.7–0.8, and the ventral margin of the leaf entire.

The *Leucophylli* are distinguished from all other members of the genus by the presence of tuberculae, and the easiest place to search for them is on the leaves. Leaf tuberculae are nearly always present, but on sporadic leaves the character may be suboptimally expressed, and in *C. aculeatus* the presence of rudimentary, inconspicuous tuberculae is a species character. Tuberculae in the *Leucophylli* are best seen in leaf profile and are easily observed under the dissecting microscope; the tuberculae then glisten. However in rare cases, the tuberculae are nondiscernable in leaf profile, as in plants of *Engel 13738* of *C. leucophyllus*. In such cases, especially if the plant is otherwise suspected of belonging in sect. *Leucophylli*, a few leaves should be removed and sectioned. Leaf sections reveal small tuberculae intermixed with mere slight projections of the tangential walls. In all cases, a careful search should be made before it is concluded that tuberculae are absent.

Members of the *Leucophylli* have a distinctive appearance when dry, even to the naked eye. Shoots are wire-like, and gaps between leaves may be observed because of the strong recurvature of leaf margins.

Key to Sect. *Leucophylli*

1. Underleaf apex with the outermost pair of processes (if present) subequal to or smaller than the primary (median) pair of processes, the underleaf summit lacking all armature except the 2 or 4 lobes (if median pair smaller [*C. aculeatus*] then never markedly and consistently so) 2

  2. Leaf cells dimorphic: most smooth and completely devoid of protuberances, but isolated distal lamina and basal lobe cells each with an obscure, small tubercula. New Zealand (North Is.; South Is. only in Punakaiki area). . . . . *C. aculeatus* (p. 161)

  2. Leaf tuberculae conspicuous and well developed 3

    3. Leaves free dorsally; leaf lobes with a uniseriate row of 4–7 cells each 1.6–3.3× longer than wide; innermost ♀ bract margins ciliate to laciniate; ♂ bracts with pocket verrucose-mamilliform in profile; plants 0.75–1.2 mm wide. New Zealand (South Is.) . . . . *C. tuberculatus* (p. 156)

    3. Leaves connate dorsally; leaf lobes with uniseriate row of 2–4 cells each 1–1.4× longer than wide; innermost ♀ bract margins entire or 1–2-dentate on ventral margin; ♂ bracts with pocket crenulate in profile; plants 2.6–3.4 mm wide. Tasmania . . . . *C. connatifolius* (p. 170)

1. Underleaf apex with outermost pair of processes (on each side at juncture of apex and lateral margin) larger than all intervening armature, which normally consists of teeth, cilia and at times laciniae, the apex mostly undivided (but the median sector in *C. leucophyllus* sometimes varying from retuse-bidentate to short bifid). Underleaves, *in situ*, 1.8–3.6× stem width; leaf lobes (if present) with uniseriate row composed of cells at most slightly elongated; ♂ bracts with pocket smooth in profile 4

  4. Leaves (of well-developed shoots) with ventral margin + armature consistently aligned toward shoot base; leaves uniformly symmetrically to weakly asymmetrically bifid, the ventral lobe subequal to or at most moderately larger than the dorsal, the dorsal lobe sometimes basal in juxtaposition to the ventral lobe, but never consistently strongly so, the apex never narrowly rounded, undivided and entire; ventral lobe of leaf terminating in a uniseriate row of (4)5–7(8) cells; underleaf apex often broadly rounded, ciliate or small dentate (outermost pair of processes excluded), often sparingly so; lateral-intercalary branches common, somewhat more abundant than terminal branches; gynoecia often on branches. Tasmania, Auckland Is., Campbell Is., Stewart Is. . . . . *C. leucophyllus* (p. 163)

  4. Leaves with ventral margin of leaf variously oriented, but never consistently aligned toward shoot base; leaves strongly asymmetrically bifid (exc. var. *symmetricus*), often appearing undivided due to strong asymmetry, the ventral lobe much larger than the dorsal, which is usually distinctly basal in juxtaposition to the ventral lobe (the apex narrowly rounded, undivided and entire in var. *obtusus*); ventral lobe of leaf terminating in a uniseriate row of 2–3(4) cells (var. *mittenianus*); underleaf apex often broadly lunate, the apex coarsely spinose dentate-laciniate, often copiously so; lateral-intercalary branches sporadic, never more common than terminal branches; gynoecia solely on main shoots, absent from branches. New Zealand (widespread) . . . . *C. mittenianus* (p. 173)

Chiloscyphus tuberculatus J. J. Engel

Chiloscyphus tuberculatus J. J. Engel, Phytologia 83: 45. 1998 (1997). Holotype: New Zealand, South Is., Southland Prov., Fiordland Natl. Park, Tutoko River, W of Milford Sound, 50 m, *Engel 18844* (F); isotype: (CHR).

Plants subisophyllous, threadlike, soft and flexuous, yet brittle, loosely creeping over substrate or in pendent sheets of bryophytes, ± whitish green, distinctly nitid when dry; shoots small, 0.75–1.2 mm wide, sometimes becoming very long, e.g., to 6.5 cm long; dried plants with leaves appearing distant and with the distal portion strongly convex to ± terete because of strongly revolute margins. Branches common, of *Frullania* type (the half-leaf deltoid and with a subcaudate apex) or, less often, of lateral-intercalary type. Stems smooth, 8–9 cells high, the cortex poorly differentiated, in 1 layer of slightly larger cells, both the cortical and medullary cells thin walled. Rhizoids in tight fascicles from stem at immediate base of underleaves, the tips sometimes digitate. Leaves opposite, subvertical to subhorizontal, not to slightly dorsally assurgent, the shoot appearing rather strongly convex in dorsal view, the leaves obliquely to widely spreading but never consistently at right angles, distant to contiguous, free dorsally, the orientation subtransverse to succubous, not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement permitting exposure of considerable stem tissue in dorsal view. Leaves broadly and strongly convex (dorsal view), but not canaliculate distally, asymmetrically narrowly to broadly ovate to subtrapezoid, conspicuously widest at the base, the ventral-basal portion of leaf moderately dilated and broadly rounded; apex symmetrically bifid to 0.3–0.35(0.4), the lobes parallel to rather strongly diverging, plane to slightly ventrally sulcate, subequal or the ventral somewhat larger but not longer, the dorsal lobe not basal in juxtaposition to the ventral lobe; lobes subcaudate to piliferous, the ventral terminating in a uniseriate row of (4)5–7 elongated cells (1.6–3.3:1); dorsal margin ± straight to broadly and slightly curved, plane to sharply reflexed, entire or with up to 6-dentate to spinose dentate-ciliate processes, the margin conspicuously long decurrent; ventral sector of leaf broadly reflexed and revealing a broad portion of dorsal surface of leaf in ventral view, the ventral margin + armature aligned toward shoot base or ventral-basal; ventral margin (1)2–4-spinose dentate-laciniate, often ciliate, rarely entire, the armature situated on the dilated sector. Lobe base and lamina often bordered by a row of longer and often narrower cells, the border sometimes ill-defined or lacking. Leaf and underleaf cells on their dorsal and ventral surfaces each with a rather large, domelike to subclavate (then constricted near its origin from cell), prominent, hyaline tubercle which collectively glisten in leaf profile; tuberculae absent on distal portion of lobes, marginal armature and some median-basal somewhat enlarged cells; leaf cells with massive, nodular or protuberant, irregularly triangular to rectangular trigones that are confluent or separated by narrow thin-walled places, the cell lumen bounded mostly by the massive trigones; median leaf cells 17–23 µm wide, 20–25 µm long; leaves with median-basal field of enlarged cells with trigones similar to those of median cells; underleaf cells all or nearly all ± isodiametric, at most with 1–2 rows of somewhat elongated cells in median-basal sector. Oil-bodies variable in number, ranging from (1–2)3–4(5–7) to 5–8(9–10) per cell, botryoidal, spherical to subspherical and 4–5.5 × 5–6 µm to ellipsoidal and 4–4.8 × 7.5–10 µm, rarely 5 × 11 µm. Underleaves considerably smaller than leaves, *in situ* 1.1–1.9× stem width, distinctly wide connate on both sides, the insertion inverted shallowly U-shaped, the underleaves rather strongly spreading, contiguous to loosely imbricate, slightly to moderately concave (ventral view), quadrate to subcuneate when flattened; apex truncate to broadly rounded, 4-lobed by prominent subcaudate to piliferous lobes of about equal size or the median pair larger, the median pair at most sporadically smaller, the lobes terminating in a uniseriate row of several elongate cells, the median sinus descending to 0.4–0.5, the underleaf sinuses of subequal depth or the median sinus shallower and then the outermost processes appear apical-lateral or lateral in position (the underleaves then appearing bifid), the apex otherwise lacking other armature; lamina margins recurved, particularly near the base, entire or with a spinose tooth on 1 or both margins. Asexual reproduction absent.

Plants dioecious. Androecia subfoliose grading to subspicate, on main shoot or rather long *Frullania*-type branches, sporadically on rather long lateral-intercalary branches, the androecia initially terminal but eventually become intercalary (the shoots often with several intercalary androecia), the androecia often long, with up to 12 pairs of bracts. Bracts moderately to distinctly smaller than leaves, the bracts suberect to obliquely spreading, ± transversely oriented, strongly dorsally assurgent, loosely imbricate, the saccate portion fused at base with opposite bract and distinctly tuberculate-mamillate in profile, the dorsal-basal portion distinctly ventricose, the apex as in vegetative leaves; lobule margin inflexed to involute, with 2–3 several-celled teeth terminating in slime papillae, the margin otherwise crenulate and sometimes with additional slime papillae; antheridia solitary, large for bract size, the stalk 19–26 cells long, biseriate. Gynoecia anisophyllous, on main shoot or rather long *Frullania*-type branches, occasionally on elongate subfloral innovations; subfloral innovations often present, from below bracts of third (lowermost) series, sometimes with several innovations per gynoecium; vestigial stem perigynium present, narrowly cylindrical to ovate, the foot of the mature sporophyte near its base, the bracts and bracteoles of innermost and second series and often accessory acuminate scales inserted on the vestigial perigynium, with 1 or both bracts of innermost series often attached on perianth tissue, the attachment of the bract often by 1 of margins (in addition to the usual basal attachment). Bracts of innermost series considerably larger than leaves, erect and ensheathing the vestigial perigynium and lower sector of perianth, free from one another, plane or with the distal portion convex, the bracts ovate, with apices deeply bifid by subcaudate lobes with margins often armed with ciliiform processes; lamina margins plane to slightly reflexed, ciliate to laciniate, the dorsal base lobulate. Bracteoles of innermost series smaller than bracts, ca. 0.6–0.65 bract area, broadly connate on 1 side and weakly so or free on the other, the bracteoles plane, quadrate to ovate; apices 2–4-lobed, the lobes acuminate; lamina margins dentate to laciniate. Bracts and bracteole with small tuberculate cells distally and with a field of enlarged smooth or tuberculate cells toward base. Perianth short to longly exserted beyond bracts, sharply trigonous for most of its length, the sides sometimes infolded, the perianths narrowly ovate to oblong, not to slightly narrowing toward the wide, deeply 3-lobed mouth; lobes undivided to obscurely to distinctly bifid, the segments,

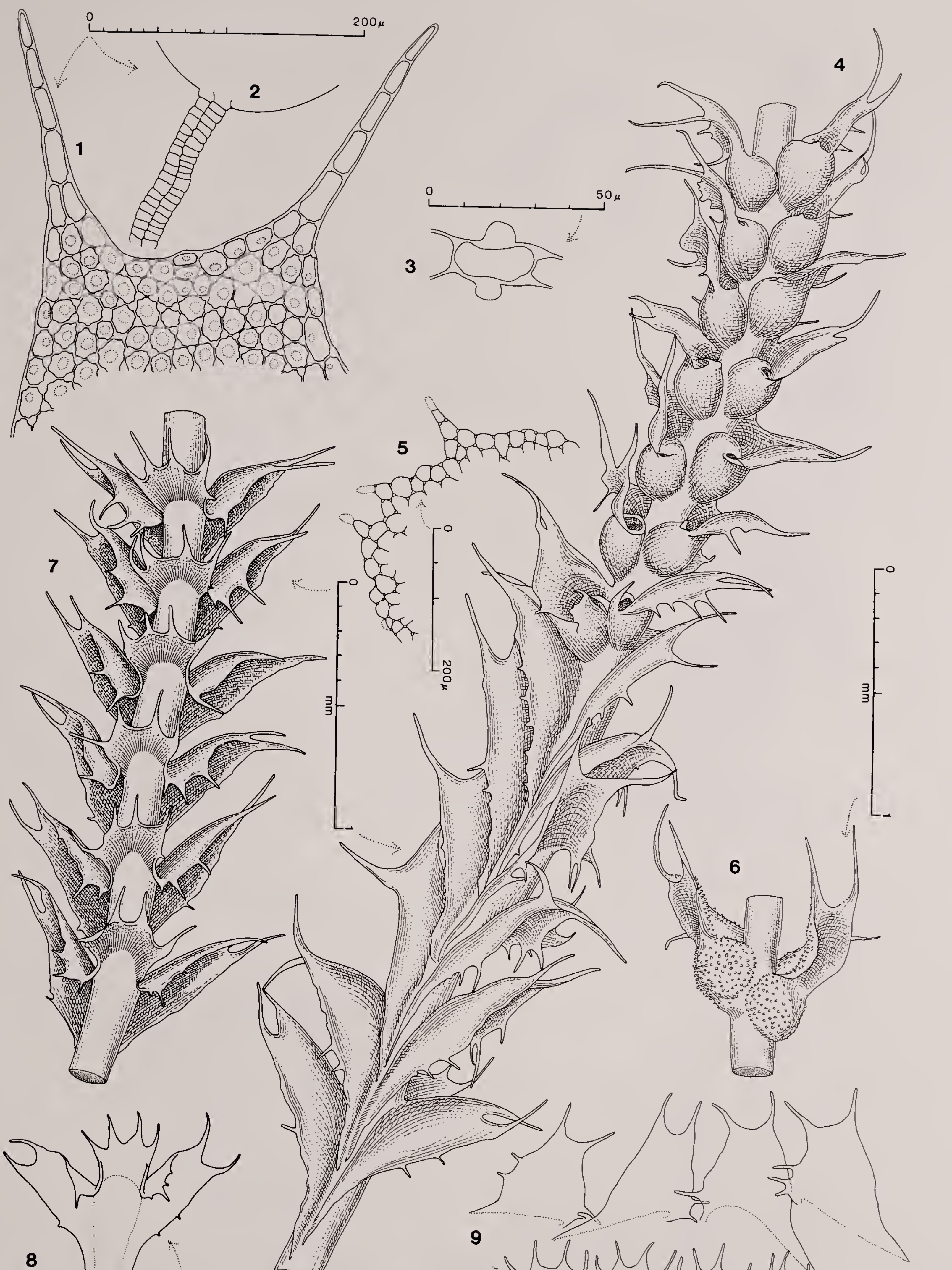

FIG. 60. *Chiloscyphus tuberculatus* J. J. Engel. **1.** Distal sector of leaf. **2.** Antheridial stalk. **3.** Leaf cross section. **4.** Portion of shoot with androecium. **5.** Margin of lobule of ♂ bract. **6.** Opposing ♂ bracts; note verrucate condition in profile. **7.** Portion of shoot, ventral view. **8.** Leaf pair and attached underleaf, partially flattened. **9.** Leaves and below, underleaves to same scale. (All from holotype.)

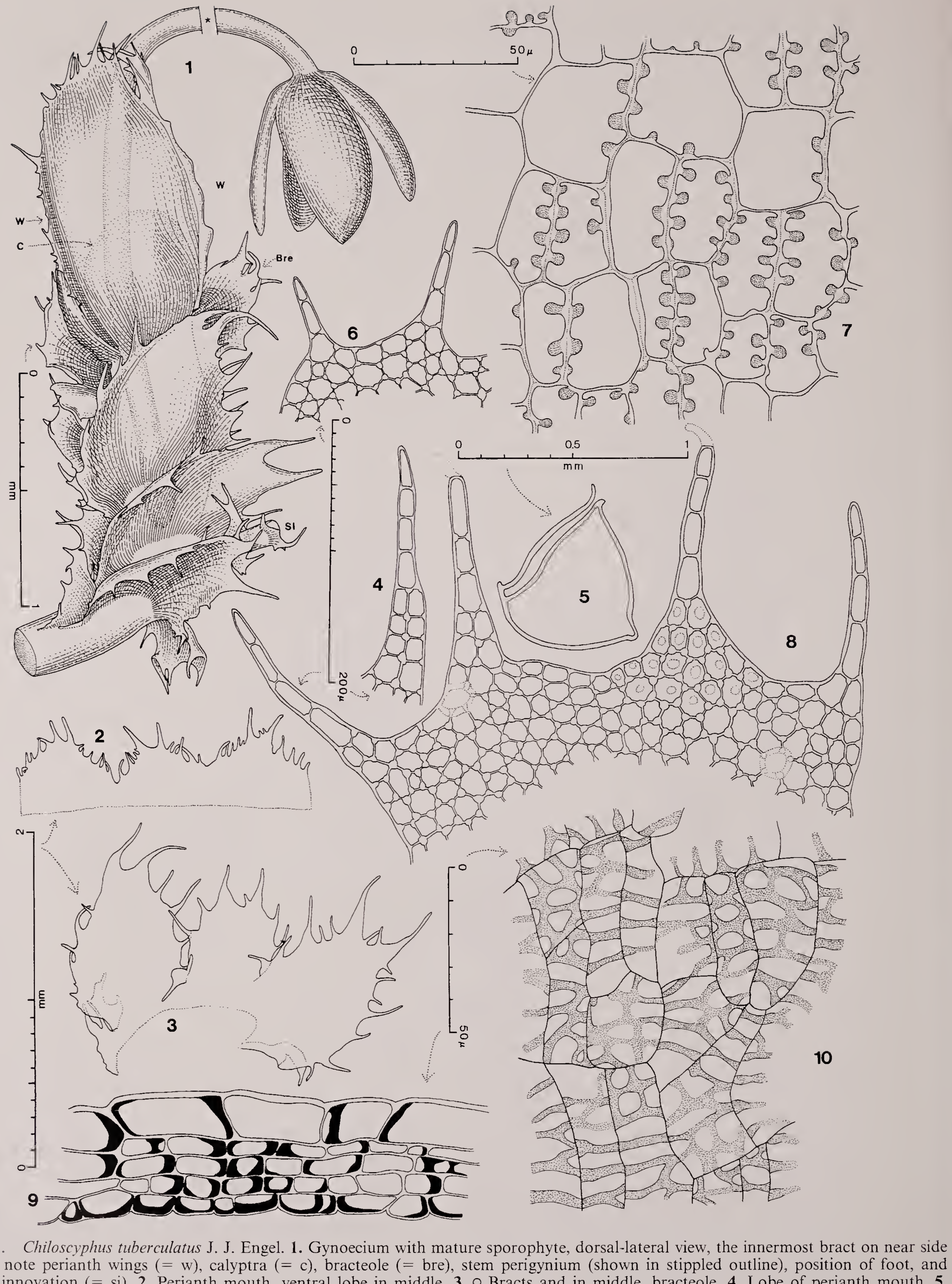

FIG. 61. *Chiloscyphus tuberculatus* J. J. Engel. **1.** Gynoecium with mature sporophyte, dorsal-lateral view, the innermost bract on near side removed; note perianth wings (= w), calyptra (= c), bracteole (= bre), stem perigynium (shown in stippled outline), position of foot, and subfloral innovation (= si). **2.** Perianth mouth, ventral lobe in middle. **3.** ♀ Bracts and in middle, bracteole. **4.** Lobe of perianth mouth. **5.** Perianth, cross section, note fusion of accessory "leaf." **6.** Basal sector of ventral margin of leaf. **7.** Capsule wall, outer layer. **8.** Distal sector of underleaf, the verrucae shown only in part; note secondary thickening of 2 cells. **9.** Capsule wall, cross section. **10.** Capsule wall, inner layer. (**1–4, 6–10,** from holotype; **5,** from *Engel 18837*, same loc.)

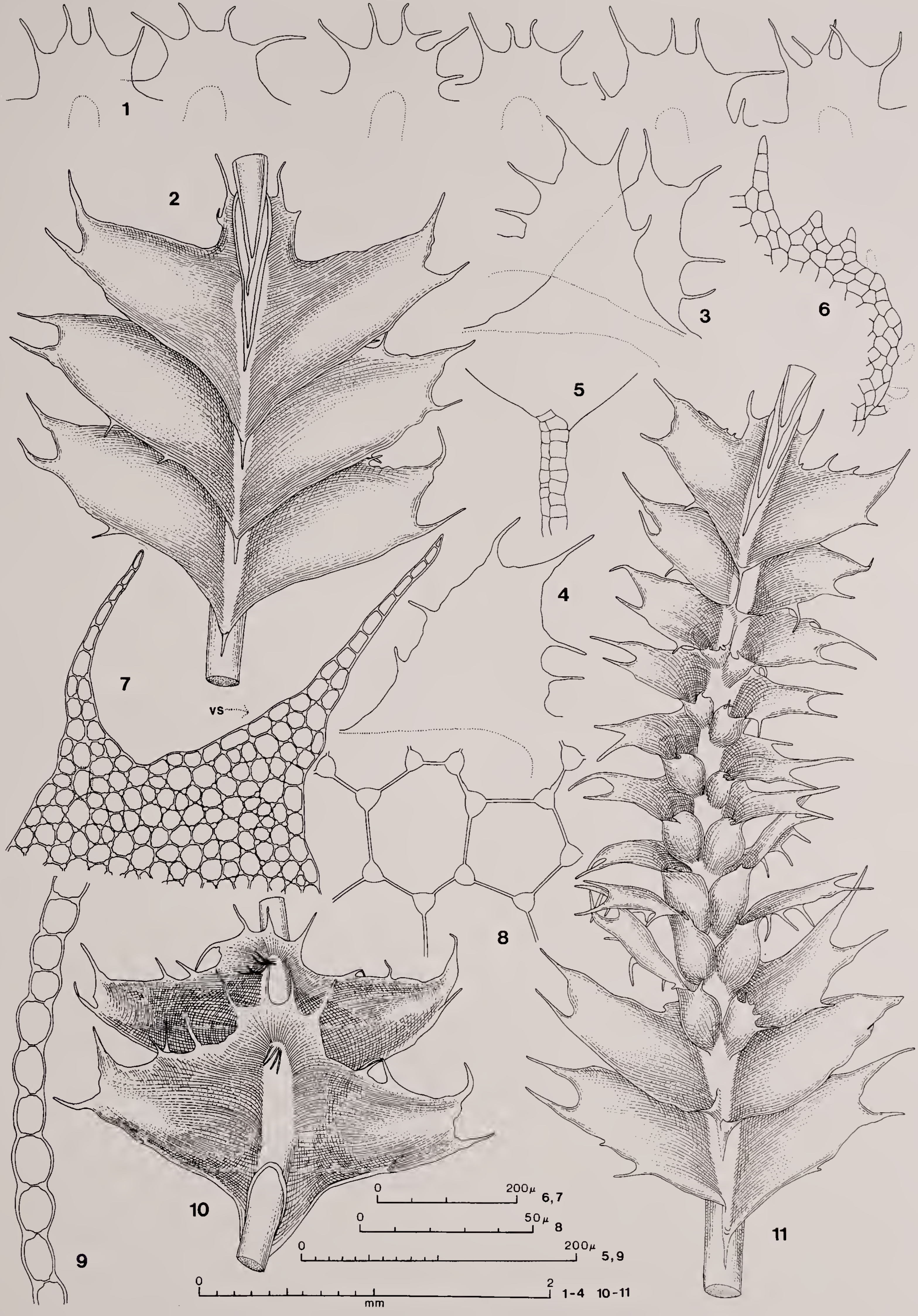

FIG. 62. *Chiloscyphus aculeatus* Mitt. **1.** Series of underleaf outlines. **2.** Sector of shoot, dorsal view. **3, 4.** Leaf outlines. **5.** Antheridium. **6.** Margin of lobule of ♂ bract. **7.** Distal portion of leaf (vs = ventral segment). **8.** Median leaf cells. **9.** Leaf, cross section through middle third. **10.** Sector of shoot, ventral view. **11.** Sector of leading shoot with androecium. (All from *Schuster 48942a*, New Zealand, North Is., Mt. Egmont Natl. Park.)

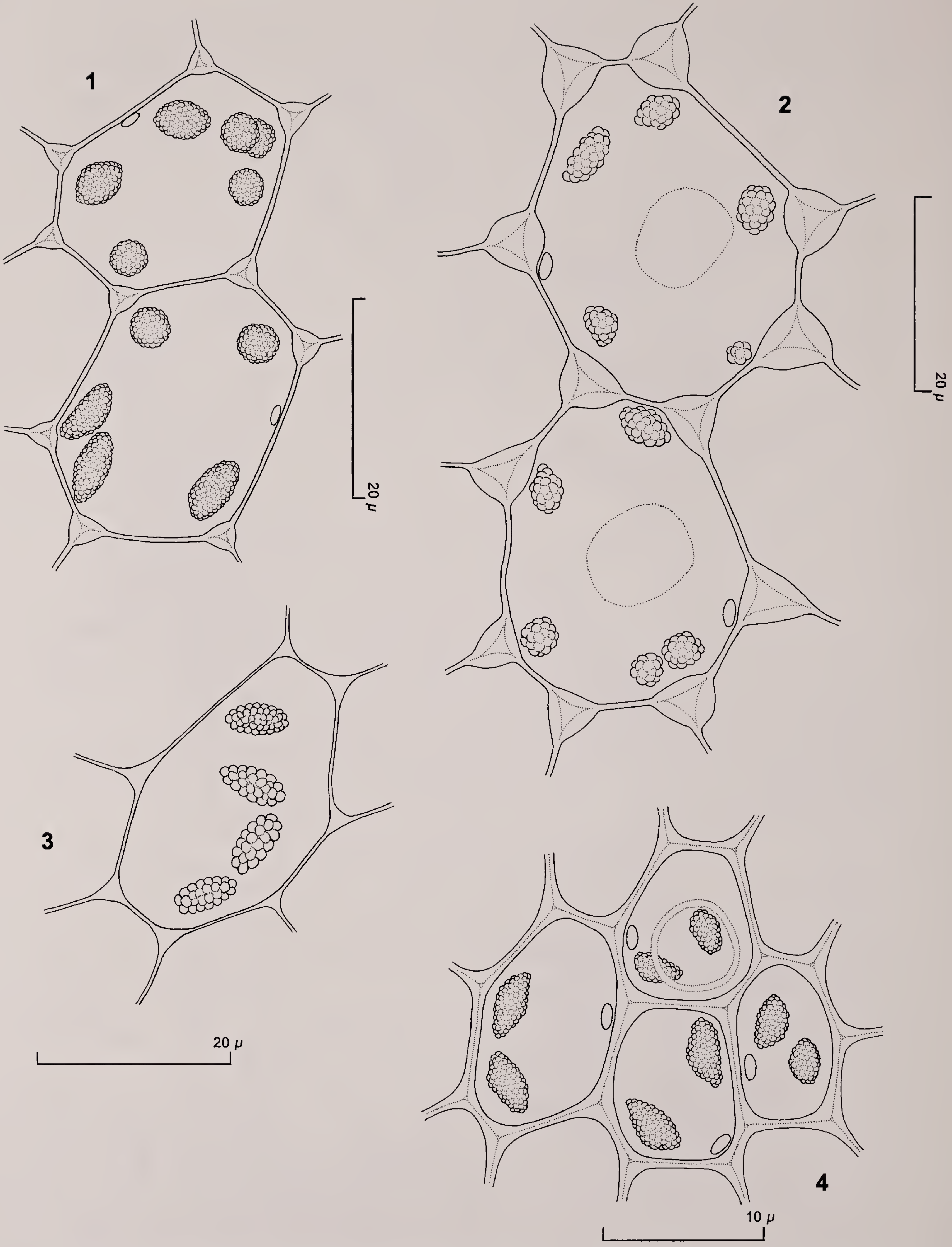

FIG. 63. Oil-bodies. **1.** *Chiloscyphus aculeatus* Mitt. Median lamina cells, the outline of a few chloroplasts included. **2.** *Chiloscyphus mittenianus* (Col.) J. J. Engel. Median lamina cells, the outline of a few chloroplasts included. **3.** *Chiloscyphus villosus* (Mitt. ex Steph.) J. J. Engel & R. M. Schust. Median lamina cells. **4.** *Chiloscyphus muricatus* (Lehm.) J. J. Engel & R. M. Schust. Median lamina cells, the outline of a few chloroplasts included; the uppermost cell with spine base indicated. (**1,** from *Engel & von Konrat 23830*, New Zealand, North Is., South Auckland Prov., Kaimai-Mamaku Forest Park, Mt. Te Aroha; **2,** from *Engel, von Konrat & Braggins 25085*, New Zealand Wellington Prov., Hawkins Hill, E of Kingston; **3,** from *Engel 23208*, New Zealand, South Is., Southland Prov., Fiordland Natl. Park, Moraine Creek Track; **4,** from *Engel & von Konrat 27811*, New Zealand, North Is., Auckland Ecological Prov., Kaimai-Mamaku Forest Park, Old Kaimai Road at the Tuakopae Stream Bridge.)

when well developed, subcaudate, the lobes otherwise spinose dentate-ciliate; keels sharp, especially distally, with keelar wings occasional, of a few cells high, sometimes armed with small teeth. Perianth cells (distal extremity excepted) on outer surface each with a prominent bulging tubercle.

Seta observed only in collapsed state. Capsule wall 32–38 µm thick, of 4–5 (locally 6) layers, (in 5 stratose capsules) equal to thickness of 1.8–3 of interior strata, or (in 4-stratose capsules) the outer layer greater in thickness than all of interior strata combined; outer layer of cells subquadrate to short subrectangular, the radial walls rather thick, with red-brown nodular to sporadically spine-like thickenings which are on some but not all longitudinal walls and only sporadically on transverse walls, the outer wall with weak tendency toward two-phase type of distribution of thickenings, (i.e., longitudinal walls with several thickenings alternating with those with few or no thickenings); intermediate and inner layer of cells subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended, often becoming semiannular; innermost layer of cells irregularly quadrate to long rectangular, with semiannular bands red brown, rather wide, numerous, sometimes nonpigmented in median portion, sometimes incomplete, often forked and anastomosing to delimit fenestrae, the radial walls with nodular thickenings occasionally present, the radial walls lacking thickened sheets of wall material.

Spores not seen. Elaters tortuous, 8.2–9.6 µm wide, the spirals 2.4–2.9 µm wide.

DIFFERENTIATION—This species and *C. aculeatus* form a closely related pair; for a discussion see that species.

VARIATION—The species is one of the most stenotypic in the genus. However, the underleaf lobes are somewhat variable in stature and position. The lateral pair is usually at the juncture of underleaf apex and lateral margin and ± equal in stature to the median pair. The outermost pair may at times exceed the size of the median pair, but never consistently so. The outermost pair often is slightly to distinctly basal to the median pair; when demonstrably basal, the underleaves appear bifid, the lamina having on each side a process lateral and not apical in position.

DISTRIBUTION AND ECOLOGY—Confined to the wet, southwestern sector of South Is., New Zealand (25–610 m), occurring north to the Otira River. It apparently is restricted to rich, wet *Nothofagus* forests in well-drained niches that receive at least moderate amounts of light (and is absent from densely shaded sites). It typically occurs loosely creeping over organic material in semi-open niches. For example, on tree trunks it may occur over decayed vegetation, while on tree bases it may grow within masses of bryophytes and hymenophylls or over *Schistochila nobilis*, *Trichocolea* sp. and *Plagiochila* sp. In particularly humid niches, such as subvertical slopes above stream courses, it occurs in pendent sheets of bryophytes. It also may be terricolous; at Cross Creek (510 m, near Haast Pass, *Engel 23109*) it grows on bryophyte covered steep slopes within a mosaic of cliffs and boulders in a *Nothofagus menziesii* forest. At Avalanche Peak Track (Arthur's Pass), plants formed weft-like, very loose mats on a bryophyte-covered embankment at the forest edge near the base of a 30–40 m high vertical waterfalls above a very humid, narrow stream system in a *Nothofagus menziesii* forest. It also may be present on damp to wet cliff faces.

SPECIMENS SEEN (selected)—**NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, Dusky Sound, Supper Cove, *Zotov s.n.* as *L. aculeata*–c. ♂ (CHR); ibid., along flat of Spey River, near W arm of Lake Manapuri, on Doubtful Sound track, 190–230 m, *Schuster 52622*–c. sporo., *52630*–c. ♂ (F); ibid., head of Lake Manapouri to Wilmot Pass, *Simpson s.n.* as *L. leucophylla* (CHR); ibid., near Lake Thompson Hut, W of Lake Te Anau, on track to George Sound, ca. 290 m, *Schuster 48297* as *L. aculeata* (F); ibid., Caswell Sound, Stillwater Camp, *Henry s.n.* as *L. leucophylla* (CHR); ibid., Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel 23220* (F); ibid., Falls Creek, near junction of Hollyford River road and Milford road, *Schuster 67-2417*–c. ♂ (F); ibid., Lake Marian Track, on Hollyford River, at foot of Mt. Christina, *Schuster 55682A* (F); ibid., Tutoko River Valley, near head of Milford Sound, *Schuster 67-3540* (F); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18837*–c. sporo. + ♂ (F). **OTAGO:** Fiordland Natl. Park, Howden–Mackenzie Track, ca. 2 mi. beyond Howden Hut, *Taylor s.n.* as *L. aculeata*–c. ♂ (CHR); ibid., trail between Gunn's Hut and Hidden Falls, ca. 30 mi. SE of Lake McKerrow, *Hatcher 555*, *699* (F). **WESTLAND:** Cascade Road, just W of Jackson River, ca. 8–12 km SW of confluence of Jackson and Arawata Rivers, 25–90 m, *Engel 22984*–c. ♂ (F); Mt. Aspiring Natl. Park, Cross Creek, 1 km N of Haast Pass, 510 m, *Engel 23109* (F); Haast Pass Road, near the summit, *Allison H 6841* as *L. leucophylla*–c. ♂ (CHR); Arthur's Pass Natl. Park, Otira River gorge, W of Arthur's Pass, ca. 305–365 m, *Schuster 48492* as *L. aculeata* (F); ibid., Lower Otira River Gorge, 2–3 mi. above Otira, ca. 455–610 m, *Schuster 67-2551A*–c. ♂ + sporo. (F); Otira Gorge, *Moore H 76pp* as *L. leucophylla* (CHR). **CANTERBURY:** Arthur's Pass, falls behind Department of Conservation Station, off Avalanche Peak Track, ca. 790 m, *Engel & von Konrat 27224* (F).

Chiloscyphus aculeatus Mitt.

Chiloscyphus aculeatus Mitt. *in* Hooker f., Bot. Antarc. Voy. 2: 140. *pl. 98*, *f. 4*. 1854. *Chandonanthus aculeatus* (Mitt.) Schiffn. *in* Engl. & Prantl, Natürl. Pflanzenfam. 1 (Abt. 3, 1 Hälfte): 1 (3). 106. 1893. *Lophocolea aculeata* (Mitt.) Hodgs. *in* Martin, Trans. & Proc. Roy. Soc. New Zealand 78: 499. 1950. Type: New Zealand, "On *Hypopterygium concinnum*," *Mr. Heward* (NY!, WELT!).

Plants threadlike, soft and flexuous, loosely creeping to ascending from substrate, pale green to yellow green, distinctly nitid when dry; shoots small, 1.8–2.2 mm wide, the shoots sometimes becoming very long, e.g., to 6.5 cm long; dried plants with leaves appearing distant and with the distal portion strongly convex to ± terete due to strongly revolute margins. Branches rather sparse, nearly exclusively of lateral-intercalary type, with *Frullania*-type branching rare and sporadic or lacking. Stems smooth, 9–10 cells high, the cortex poorly differentiated, in 1(2) layers of smaller cells with slightly thickened walls. Rhizoids colorless, in tight fascicles from stem at immediate base of underleaves, the tips often digitate. Leaves opposite, horizontal, the shoot appearing flat in dorsal view, the leaves widely spreading, loosely imbricate, strongly connate dorsally, the connation several cells high and often forming a trough, the connation often long-decurrent on the stem; leaves with orientation strongly succubous, not recurved at ventral end, the leaf arrangement covering the stem in dorsal view except for narrow V-shaped sectors. Leaves broadly and moderately convex (dorsal view), the distal portion at most moderately convex, sometimes nearly plane; leaves asymmetrically trapezoid, conspicuously widest at the base, the ventral-basal portion of leaf at most moderately dilated, the ventral margin otherwise ± straight throughout, the dorsal-basal extremity dilated and forming a narrowly acute sector oriented toward shoot base; apex bifid to 0.2–0.25(0.3), the lobes often broken, parallel to rather strongly diverging, the ventral lobe frequently oriented toward shoot apex, the ventral mostly larger but only occasionally longer than the dorsal, the dorsal lobe sporadically basal in juxtaposition to the ventral lobe, the lobes occasionally subequal but never consistently so; lobes subcaudate to piliferous, the ventral terminating in a uniseriate row of 5–7(8) elongated cells (1.3–2.8:1); dorsal margin distally ± straight but near base defining an incurved line, the margin plane to moderately reflexed, entire or with 1–3 ciliiform processes; ventral sector of leaf reflexed and at times revealing a rather broad portion of dorsal surface of leaf in ventral view, at times revealing little if any of dorsal surface, the ventral margin + armature with alignment variable: grading from apical-ventral to ventral-basal, the ventral margin with 1–3 ciliiform processes. Lobe bases and lamina sometimes bordered by an ill-defined row of longer and often narrower cells. Cells of leaf mostly smooth, biconvex and without protuberances of any sort, but scattered, isolated distal lamina and basal lobe cells with a rudimentary, small, obscure tubercle, with trigones knot-like, the cell lumen usually bounded mostly by the relatively long thin walls between trigones, the trigone widths and the length of the intervening thin walls occasionally ± equal; median leaf cells 23–28 µm wide, 26–38 µm long; leaves with an ill-defined median-basal field of enlarged cells with trigones similar to those of median cells; surface faintly striate. Oil-bodies hyaline to pale smoky grey, 4–8 per cell, coarsely papillose, elliptic to ± fusciform, at times mostly globose, 8.8–10.8(11.8) × 3.9–5.9 µm, a few 6.9 × 3.9 µm. Cells of underleaf with tuberculae as in leaves, the cells isodiametric at least in distal half, sporadic or clusters of cells in basal half (especially median-basal) slightly elongated. Underleaves considerably smaller than leaves, *in situ* 2–3.5× stem width, distinctly wide connate on both sides, the insertion inverted shallowly U-shaped, the underleaves strongly spreading, occasionally at right angles to stem, distant to contiguous, slightly to moderately concave (ventral view), quadrate to subcuneate when flattened; apex broadly and often only slightly rounded, 4-lobed by prominent subcaudate to piliferous lobes of about equal size, or if median pair smaller, then never markedly and distinctly so, the outermost processes appearing apical-lateral in position, the lobes often broken, terminating in a uniseriate row of several elongate cells, the median lobes sometimes with an accessory ciliiform process toward the base, the lobe margins otherwise entire, the median sinus descending to 0.3–0.5, normally shallower than outermost sinuses, the sinuses rarely subequal, the apex otherwise lacking other armature; lamina margins plane to moderately recurved, entire or at times with a spinose tooth. Asexual reproduction absent.

Plants dioecious. Androecia subfoliose grading to subspicate, on main shoot or on rather long lateral-intercalary branches, initially terminal but eventually become intercalary (the shoots often with several intercalary androecia), the androecia rather short and with to 6 pairs of bracts per androecium or long and with to 12 pairs of bracts. Bracts moderately smaller than leaves, suberect to widely spreading, ± transversely to subsuccubously oriented, strongly dorsally assurgent, loosely imbricate, the saccate portion distinctly fused at base with opposite bract, smooth in profile, the dorsal-basal portion distinctly ventricose, the apex as in vegetative leaves except for greater lobe asymmetry; lobule margin inflexed to involute, with 1–3 several celled, often spinose teeth not terminating in slime papillae, the margin otherwise with additional sessile or stalked slime papillae; antheridia solitary, the stalk rather short, 9–10 cells long, biseriate. Gynoecia anisophyllous, on main shoot or rather long lateral-intercalary branches, often on elongate subfloral innovations issuing from unfertilized gynoecia; vestigial stem perigynium present, narrowly cylindrical, the foot of the mature sporophyte near its base, the bracts and bracteole of innermost series inserted on the vestigial perigynium but never on perianth tissue, the attachment of the bract often by 1 of margins (in addition to the usual basal attachment). Bracts of innermost series considerably larger than leaves, erect and ensheathing the vestigial perigynium and lower sector of perianth, connate dorsally, convex, the bracts ovate, distinctly narrowed distally, with apices deeply bifid by acuminate lobes with entire margins; lamina margins broadly reflexed, the margins ciliate to laciniate, the armature on ventral margin larger. Bracteoles of innermost series smaller than bracts, very broadly and subequally connate on both sides, the bracteoles slightly concave (ventral view), subquadrate to subovate; apices 4-lobed, the lobes acuminate, the median pair sparingly ciliate; lamina margins dentate to laciniate. Bracts and bracteoles with a field of enlarged cells toward base. Perianth longly exserted beyond bracts, sharply trigonous throughout, narrowly oblong to elliptic, not to slightly narrowing toward the wide, deeply 3-lobed mouth; lobes obscurely to distinctly bifid, the segments subcaudate, the lobes otherwise spinose dentate-ciliate; keels sharp, especially distally, with keelar wings rather common, of a few to several cells high, sometimes armed with small teeth or cilia.

Seta observed only in collapsed state. Capsule elliptic, 40–42 µm thick, of 4–5 layers, the outer layer of cells equal to thickness of 1.9–2.5 of interior strata; outer layer of cells subquadrate to short subrectangular, the radial walls with red-brown nodular thickenings which are mostly on longitudinal walls and only sporadically on transverse walls, the outer wall with no tendency toward two-phase type of distribution of thickenings; intermediate layers of cells on the whole slightly thicker than inner layer, the intermediate layers with vertical thickenings often considerably tangentially extended, often becoming semiannular; innermost layer of cells irregularly quadrate to long rectangular, with semiannular bands red brown, numerous, sporadically nonpigmented in median portion, sometimes incomplete, often forked and anastomosing to delimit fenestrae, the radial walls with nodular thickenings occasional, particularly at cell ends, the radial walls lacking thickened sheets of wall material.

Spores 11.5–11.9 µm, yellow brown, thin, with faint, dense, low but sharply defined, close papillae and short-vermiculate markings, the spore:elater diameter ratio 1.1–1.3:1. Elaters tortuous, 9.1–10.1 µm wide, the spirals 1.9–2.4 µm wide.

DIFFERENTIATION—*Chiloscyphus aculeatus* has a checkered history of recognition. Mitten (1854–55, p. 140) described the species based on "a few fragments," stating for provenance only "New Zealand: creeping over *Hypopterygium concinnum*." Stephani (1898–1924 [1908], p. 263) indicated that the species was not distinct from *L. leucophylla*, and Hodgson (1943, p. 49) agreed, but was not convinced, commenting (p. 49) that she "would not say that he (Stephani) was entirely wrong." Hodgson (1953) recognized *Lophocolea aculeata* and listed specimens from North, South, and Stewart Islands. However, Hodgson, (1962, p. 112) later altered her concepts, remarking "I am now constrained to agree with Stephani that *L. leucophylla* and *L. aculeata* are one and the same."

Leaves of *C. aculeatus* appear smooth, especially under the dissecting microscope, and therefore may quite easily be mistakenly placed in sect. *Connati.* Because of this potential confusion, I have included this species in the key to sect.

TABLE 13. Comparison of *Chiloscyphus aculeatus* with some species of sect. *Connati*.

Character	*C. aculeatus*	*C. suboppositus*	*C. edentatus*
Shape of ventral lobe	subcaudate to piliferous	medium acute to acuminate	narrow to medium acute to subacuminate, sometimes apiculate
No. of cells of ventral segment uniseriate row	5–7(8) elongated cells	1–3, at most, slightly elongated cells	2–4 isodiametric cells
Underleaf apex	0.3–0.5-fid	0.15–0.35-fid	retuse-bidentate to at most 0.3-fid
Armature of leaf margins	often each with 1–3 ciliiform processes	ventral margin rarely with a tooth, otherwise entire	entire

Connati; doubtful plants should be tested against both keys. The leaf cells of *C. aculeatus*, however, are actually dimorphic—most are smooth and completely free of verrucae, but scattered distal lamina and basal lobe cells have a small, rudimentary verruca. Unlike other members of the *Leucophylli*, leaf verrucae are best observed by viewing several dissected leaves under the compound microscope. The verrucae are so obscure that I repeatedly utilized a phase contrast compound microscope to confirm their presence in different collections.

It is useful to be aware of the distribution of other members of the *Leucophyli* when working with New Zealand populations. The only other species in the region of North Is. that *C. aculeatus* occurs is *C. mittenianus* (*C. tuberculatus* is a South Is. plant, see below). Plants of *C. aculeatus* are highly nitid, frequently have subfloral innovations from unfertilized gynoecia and have a nonprickly appearance vs. plants that are dull-textured, only occasionally have subfloral innovations and have a prickly appearance in *C. mittenianus*.

Chiloscyphus aculeatus has interesting relationships with sect. *Connati*, and exhibits some affinities with *C. suboppositus* and *C. edentatus* of the latter section. Since leaf verruca are so obscure in *C. aculeatus*, I include Table 13 to distinguish these species.

NOTES—1) Hodgson's (1953) concept of *C. aculeatus* encompassed *C. tuberculatus* since she included South Is. plants. However, the focus of her description is on *C. aculeatus*: e.g., leaves dorsally connate and leaf "papillae" mostly absent. Furthermore, the perianth is based on a specimen of that species (*fide Allison H744* CHR!).

2) The oil-body data of *C. aculeatus* and report of that plant from the South Is. in Stewart (1978) are based upon a misdetermined specimen of *C. spinifer* (*fide* CHR 266142).

DISTRIBUTION AND ECOLOGY—Endemic to New Zealand, and known almost exclusively from North Is. (245–950 m). The species appears to be more common at lower elevations, where it occurs in rich *Agathis* forests, in *Agathis–Leptospermum scoparium* succession zones, or in mixed broadleaf forests dominated by *Beilschmiedia* and *Weinmannia* or of *Weinmannia silvicola* and *Syzygium maire*. It also is known from a few sites at higher elevations; for example, it occurs in wet, mature *Dacrydium–Metrosideros–Weinmannia* forests at 610 m on the flanks of Mt. Egmont, in swampy areas with *Libocedrus*, *Nothofagus*, and *Metrosideros* (ca. 950 m on Ohakune Mtn. Road, *Engel 21333*), and in *Nothofagus Dacrydium cupressinum–Podocarpus totara* forests (650–920 m, Waikareiti Track in Urewera Natl. Park, *Engel 20516*). The species occurs in semi-shaded to moderately open sites, and grows loosely terricolous on the forest floor or in niches very near the floor, such as over exposed vertical roots and on tree bases; the species tends to occur as a constituent of mounds or masses of bryophytes. At Whareorino Forest in the Herangi Range (near tributary of Awakino River, SW of Te Kuiti township) plants formed soft, pure, large masses ca. 1 m above the base of *Dicksonia* and grew stiffly away from the substrate. The site is a narrow stream valley under a canopy of *Melicytus ramiflorus*, *Cyathea smithii* and *Pseudopanax arborea*. In deeply shaded, protected niches, such as in a forest dominated by stunted *Nothofagus menziesii*, associated with *Dracophyllum* and *Quintinia serrata* on the south-facing slope of Mt. Te Aroha, plants form loose, pure, tufts ± pendent from vertical banks.

On South Is. *C. aculeatus* is known only from the Punakaiki area (ca. 25 m at Bullock Creek in Paparoa Natl. Park, *Engel 21570*). At this site the species forms huge mounds at the forest edge near the roadside in an area of limestone outcrops and cliffs in a mixed broadleaf forest. Many predominantly North Is. species of both vascular and nonvascular plants have their southern limits in the mild lowland coastal forest of Westland and also in the Nelson region which shares a similar climate (David Glenny, in litt.). Examples are *Rhopalostylis sapida* and *Metrosideros robusta*.

SPECIMENS SEEN (selected)—**NEW ZEALAND. SOUTH ISLAND. NELSON PROV.:** Paparoa Natl. Park, Bullock Creek Road, along Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel 21570*–c. sporo. (F). **NORTH ISLAND. WELLINGTON:** Akatarawa, *Braggins 84/427B* as *L. leucophylla* (AK); Tararua Mtns., Akatarawa Saddle, *Zotov s.n.* (CHR); Tongariro Natl. Park, ca. 8 km from Ohakune on Ohakune Mtn. Road, ca. 950 m, *Engel 21333* (F). **HAWKE'S BAY:** Inland from Wairoa, *Lane s.n.* as *L. leucophylla*–c. ♂ (CHR). **TARANAKI:** Mt. Egmont Natl. Park, near Stratford Mtn. Road, E slope of Mt. Egmont, ca. 610 m, *Schuster 48942A*–c. ♂ (F); Pukeiti Bush, near New Plymouth, *Hatcher 416* (F). **GISBORNE:** Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20516*–c. sporo. + ♂ (F). **SOUTH AUCKLAND:** Mamaku, near Rotorua, *Wallace s.n.* as *L. leucophylla*–c. ♂, *s.n.* as *L. leucophylla*–c. sporo. (CHR). Herangi Range, Whareorino Forest, near tributary of Awakino River, W of Leitchs Road, and SW of Te Kuiti township, 285 m, *Engel & von Konrat 23942* (F); Mt. Te Aroha, S facing slope, 880–890 m, *Engel & von Konrat 23830* (F). **NORTH AUCKLAND:** Waipoua Kauri Forest Preserve, Matua Ngahere Kauri area, *Schuster 67-1329, 67-1342, 67-1353* (F); Waipoua Forest, *Schuster 51934* (F); ibid., *Allison H 655a* as *L. leucophylla* (CHR); ibid., on Toronui Track, *Allison H 744* as *L. leucophylla*–c. per. (CHR); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21120*–c. ♂ (F); Manginangina Reserve, Puketi Kauri Forest, S of Kaeo, *Schuster 67-1006*–c. ♂ (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel 21024* (F); Mangamuka Range, ca. 395 m, *Braggins 84/36* (AK); Mangamuka Gorge, ca. 245 m, *Braggins 84/31f* (AK); Mangamuka Walkway, Maungataniwha Range, ESE of Kaitaia, saddle on State Highway 1, 390 m, *Engel 20958* (F).

Chiloscyphus leucophyllus (Hook. f. & Taylor) Gottsche, Lindenb. & Nees

Jungermannia leucophylla Hook. f. & Taylor, London J. Bot. 3: 384. 1844, *non J. leucophylla* (Lehm.) Hook. f. & Taylor *in* Hooker f., Bot. Antarc. Voy. 1 (2): 424. 1847 (= *Pachyschis-*

tochila). *Chiloscyphus leucophyllus* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 181. 1845. *Lophocolea leucophylla* (Hook. f. & Taylor) Mitt. *in* Hooker f., Bot. Antarc. Voy. 2: 138. 1854, *non L. leucophylla* Gottsche, Lindenb. & Nees, Syn. Hep. 155. 1845, *nom. inval.* Type: Auckland Creek, 1840, *Hooker* (BM!–c. ♂, E!–c. ♂, FH!–c. ♂).

Lophocolea leucophylla Gottsche, Lindenb. & Nees, Syn. Hep. 155. 1845, *nom. inval.* (Art. 34.1; see Engel, 1991d). Type: Tasmania, sub "Van Diemens Land, *Jungermannia leucophylla* Taylor *in* Hb. Greville," *sin. coll.* (E!, "Greville Herb.;" FH = absens).

Lophocolea verrucosa Steph., Bull. Herb. Boissier 6(11): 938. 1906 (= Spec. Hep. 3: 118), *syn. fide* Engel (1991d). *Chiloscyphus verrucosus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 425. 1985 (1984). Lectotype (*fide* Engel, 1991d): Tasmania, Frenchman's Cap, 1893, *Moore 32* (G!–c. ♂).

Lophocolea fulva Steph., Spec. Hep. 6: 273. 1922, *syn. fide* Engel (1991d). *Chiloscyphus fulvus* (Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 415. 1985 (1984). Type: Auckland Creek, *Cockayne 815* (ex hb. Berlin) (CHR!, G!).

Plants subisophyllous, with a rather spiny appearance, soft and flexuous to stiff and wiry, ascending to erect, light green to pale yellow green, often becoming pale brown in basal portion, distinctly nitid when dry; shoots rather small to medium, (1)1.5–2.4 mm wide; dried plants with a distinct appearance: the basal portion of leaves broad, the distal portion narrowed and appearing ± terete due to strongly revolute margins. Branches common, of lateral-intercalary and *Frullania* types (the half-leaf of similar shape to vegetative leaves), the lateral-intercalary branches somewhat more prevalent. Stems smooth, 10–13 cells high, the cortex moderately differentiated, in 1–2 layers of somewhat smaller and thicker walled cells; medullary cells thin walled. Rhizoids in tight, cylindrical fascicles from stem at immediate base of underleaves, the tips sometimes digitate. Leaves opposite, horizontal (except sometimes near base, which may be somewhat dorsally assurgent), the shoot appearing distinctly flat in dorsal view, the leaves spreading at right angles or nearly so, loosely to densely imbricate, free dorsally, the orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement practically covering the stem in dorsal view except for a very narrow median strip. Leaves broadly and strongly convex (dorsal view) the distal portion of leaf canaliculate to tubular-terete (best observed in ventral view); leaves asymmetrically deltoid to subovate, conspicuously widest at the base, the ventral-basal portion of leaf sometimes moderately dilated and broadly rounded; apex symmetrically to weakly asymmetrically short bifid, the ventral lobe subequal to or at most moderately larger than the dorsal, the dorsal lobe sometimes basal in juxtaposition to the ventral lobe, but never consistently strongly so and never absent altogether; lobes acuminate to subcaudate, the ventral terminating in a uniseriate row of (4)5–7(8) at most slightly elongated, thick-walled cells; dorsal margin ± straight to broadly and slightly curved, usually strongly reflexed to revolute and often forming a cnemis, the margin sometimes plane, 3–7(9)-spinose dentate, rarely entire or with 1–2 processes; ventral sector of leaf broadly reflexed to subrevolute and revealing a broad portion of dorsal surface of leaf in ventral view, the ventral margin + armature aligned toward shoot base (often plane and not reflexed in suboptimal, lax plants); ventral margin (2)3–5(6) sharply spinose dentate-laciniate, rarely entire or with a single process. Leaf cells on their dorsal and ventral surfaces (and cells of both surfaces of underleaf) each with a rather small, domelike, prominent, hyaline tubercle which collectively glisten in leaf profile; tuberculae absent on distal portion of lobes, marginal armature and some median-basal inflated cells; leaf cells with walls thin, trigones knot-like, median leaf cells 23–31 µm wide, 30–37 µm long; leaves and underleaves with median-basal field of inflated cells with trigones similar to those of median cells. Oil-bodies 2–3(5) per cell, elliptic to rather irregularly linear, ± weakly botryoidal, 4.2–4.5 × 8–10(11) µm, some 3.5 × 6.5 µm. Underleaves a little smaller than leaves, *in situ* 1.8–2.9× stem width, very broadly connate on both sides, the insertion inverted U-shaped, the underleaves rather strongly spreading, imbricate, concave to decidedly cupulate (ventral view), the distal portion often broadly reflexed, the underleaves (flattened) subrectangular (the longer axis at right angles to stem) to broad oblate; apex mostly undivided and truncate to broadly rounded, the juncture of apex and lateral margin on each side with a prominent laciniiform to subcaudate to sharply lobe-like process, the intervening apical margin with a varying number of much smaller ciliiform or dentiform processes (the median pair true segments?), the median armature commonly consisting of a pair of processes with the area between sporadically retuse to short bifid; lamina margins broadly recurved, the opposing margins + armature often aligned toward one another, the margins dentate-laciniate. Asexual reproduction absent.

Plants dioecious. Androecia subfoliose grading to subspicate, on main shoot or short to rather long lateral-intercalary branches, sporadically on rather long *Frullania*-type branches, the androecia initially terminal but eventually becoming intercalary, mostly rather short and with 6 or less pairs of bracts per androecium. Bracts moderately to strongly smaller than leaves, suberect to obliquely spreading, subtransversely to subsuccubously oriented, rather strongly dorsally assurgent, loosely to closely imbricate, the saccate portion fused toward base with opposite bract, the dorsal-basal portion distinctly ventricose and smooth in profile (at most with exposed walls of cells convex); lobule margin involute, crenulate and with copious slime papillae; antheridia solitary, small for bract size, the stalk biseriate. Gynoecia anisophyllous, on main shoot or leading lateral-intercalary branches or, less often, *Frullania*-type branches; subfloral innovations sometimes present, from below bracts of second or third (lowermost) series; vestigial stem perigynium present, the bracts and bracteoles of innermost series inserted on the vestigial perigynium. Bracts of innermost series often similar in size to leaves or smaller, the bracts of series immediately below larger, those of innermost series erect and ensheathing perianth, free from one another or weakly connate dorsally, broadly convex, the distal portion canaliculate, the bracts ovate, with similar basic form of vegetative leaves; lamina margins spinose dentate-laciniate, the dorsal margin sharply reflexed, the ventral ± plane. Bracteoles of innermost series smaller than bracts, ca. 0.5–0.55 bract area, rather broadly connate on both sides or broadly connate on 1 side and weakly so or free on the other, strongly concave (ventral view), suborbicular; apices slightly and broadly rounded, with a pair of subcaudate processes at juncture of apex and lateral margin, the intervening portion of apex with 2 small teeth; lamina margins spinose dentate-laciniate. Bracts and bracteole with small, tuberculate cells distally, and with a very large field of inflated smooth cells in basal half. Perianth longly exserted beyond bracts, sharply trigonous for most of its length, the sides often infolded, particularly in older perianths, the perianths narrowly oblong, not narrowing toward the wide, shallowly 3-lobed mouth;

lobes undivided and broadly rounded, spinose dentate and with a few small laciniae; keels sharp, in section multicellular, with keelar wings occasional, of a few cells high, sometimes with a small tooth. Perianth cells (distal and basal extremities excepted) on outer surface each with a prominent bulging tubercle, the inner surface smooth. Calyptra small, extending to ca. 0.4 the perianth length at maturity.

Seta observed only in collapsed state. Capsule 34–36 µm thick, of 4–5 layers, the outer layer of cells 18–19 µm thick, equal to 2–2.1 of interior strata or greater in thickness than all of interior strata combined; outer layer of cells subquadrate to short subrectangular, the radial walls with red-brown nodular to spine-like thickenings which are often irregularly confluent at the base, the thickenings nearly all on longitudinal walls, rarely on transverse walls, the longitudinal (and in part transverse) walls often with short to long moderately thickened sheets of wall material, the sheets and nodules, when together, appear irregularly sinuous, the basal cells with both longitudinal and transverse walls with decidedly thickened continuous sheets of wall material; intermediate and inner layer of cells subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended, often becoming semiannular; innermost layer of cells quadrate to long rectangular, with semiannular bands red brown, rather wide, close and numerous, sometimes nonpigmented in median portion, sometimes incomplete, often forked and anastomosing to delimit fenestrae, the radial walls with nodular thickenings often present, sometimes of a darker wall material and appearing to "anchor" the bands to the radial walls, the radial walls often with moderately thickened sheets of wall material.

Spores 11–14.4 µm, pale yellow brown, thin, with faint, dense, low, close, papillose and occasionally short-vermiculate markings, spore:elater diameter ratio (1)1.2–1.4:1. Elaters tortuous, 9.1–11 µm wide, the spirals 2.4–3.4 µm wide, loosely wound.

DIFFERENTIATION/VARIATION—Leaf margins are nearly always armed, and often copiously so, and underleaf margins are spinosely dentate-laciniate (Fig. 65: 1, 12). Interestingly, on any given shoot there is remarkably little variation in number of teeth on either the dorsal or ventral margin. However, suboptimal plants vary both in the amount and magnitude of the armature. Such plants, for example, usually have 1–3 small teeth on the dorsal and ventral margins and have smaller underleaf armature than in better developed plants. Leaf margins are rarely entire, and underleaf margins are even more conservative in their loss of armature, virtually never being entire-margined.

The orientation of the ventral margin toward the shoot base is an important diagnostic feature of the species (Fig. 65: 1), and one that will distinguish it from *C. mittenianus*. The ventral margins rarely are oriented otherwise, such as with orientation ventral or toward the shoot apex. The latter condition occurs in easily recognizable suboptimal plants of two types: 1) larger, lax plants with only slightly concave underleaves and weakly imbricate leaves (such shoots occasionally are intermixed with better developed plants); and 2) small, wire-like plants with leaf margins sparsely armed and leaves weakly imbricate. The latter should be treated carefully, since they may be confused with *C. suboppositus*.

Small wire-like plants with leaf armature sparse or lacking represent an extreme of the suboptimal phase. Such populations are rather rare, and must be treated with great care because of possible confusion with *C. connatifolius*. Two plants serve as useful examples since one (*Norris 29909*) is an extreme phenotype in having leaf margins entire or sporadically with a tooth, while the other (*Norris 26745*) still retains 1–2 small teeth per margin. Both populations have mostly ovate underleaves, the often entire margins broadly curved toward the summit. Some shoots have underleaves completely devoid of apex and marginal armature except for two teeth at the summit, while other shoots have such underleaves accompanied by those with lateral armature and accessory armature at the apex. The orientation of the ventral margin + armature is variable: some shoots have alignment mostly toward the shoot base, while others have alignment ventral or toward the apex. Dorsal connation of leaves is sporadic, and fusion occurs between the extremity of a leaf on one side with the dorsal surface of an opposed leaf. In no case is fusion consistent throughout any given shoot—connate leaves are always accompanied by free opposed leaves. Also, leaf connation occurs only between 2 subopposed leaves, and never involves 3 leaves as commonly occurs in *C. connatifolius* (see Fig. 67: 3, and Note 1).

Such suboptimal plants express, albeit somewhat inconsistently, some of the characters found in optimal *C. connatifolius* (see Fig. 68: 3, 4), and confusion with that species therefore ensues. However, a crucial suite of characters is retained in the suboptimal phase of *C. leucophyllus* (they are incorporated into the key below), and should be used to distinguish the species. The student should bear in mind those characters representing optimal *C. leucophyllus* even though they are expressed inconsistently in weak plants. For example, careful search will reveal, at least on some shoots, some underleaves with a pair of lateral processes at the summit that exceed the magnitude of intervening armature. That character, even though inconsistent, never occurs in *C. connatifolius*. The well-developed and suboptimal phases of *C. leucophyllus* are separable from *C. connatifolius* as follows.

Key to the *Chiloscyphus leucophyllus–C. connatifolius* Complex

1. Leaves consistently connate dorsally, a leaf commonly fused with 2 others (cf. Fig. 67: 3); underleaves with cells all large, without a distal field of small, ± isodiametric cells; shoots large, 2.6–3.4 mm wide . . . *C. connatifolius*
1. Leaves usually free dorsally, but if connate (rare and sporadic on weak plants), then fusion only between 2 subopposed leaves; underleaves with a distal field of small, ± isodiametric cells; shoots small, 1.5–2.4 mm wide . . 2
    2. Dorsal and ventral margins of leaf each consistently armed with at least two processes; underleaf summit with 2 lateral processes that exceed the size of all intervening armature; ventral margin + armature consistently aligned toward shoot base; shoots 1.5–2.4 mm wide . . . . . . well-developed *C. leucophyllus*
    2. Dorsal and ventral margins of leaf each entire or 1–2-dentate; underleaf summit bidentate, with lateral armature sporadic or lacking; ventral margin + armature alignment variable, at times toward shoot apex; shoots 1–1.6 mm wide . . . . suboptimal extremes of *C. leucophyllus*

The underleaves usually have a discernable shape when flattened. However, smaller plants sometimes have amorphous underleaves, the leaf and underleaf margins imperceptibly merging, the lamina of the latter a mere rounded projection.

The most commonly expressed form of underleaf apex consists of two lateral processes, each at the juncture of apex and lateral margin, and a pair of small teeth (? = segments) in the median sector of the apex. This is the simplest form of apical armature, and *in situ* appears much like Fig. 64: 12, while flattened like Fig. 64: 9 or smaller. Underleaves with progressive increase in apical armature are depicted in, respectively, Fig. 65: 14, 3, and 8. A discernible sinus usually is lacking between the median pair of processes. However, with increased stature of that pair, the apex grades from retuse-bidentate to short bifid.

In rare cases, leaves of *C. leucophyllus* appear smooth in profile; see comments under sect. *Leucophylli* for treatment of such specimens (p. 155).

Notes—1) The name *Lophocolea verrucosa* Steph. was not used in the literature subsequent to the original description, despite several Rodway collected and determined specimens bearing this epithet in HO. Rodway (1916) used the name *L. leucophylla* and indicated (p. 50) that "*L. verrucosa*, St., appears not distinct."

2) Hodgson recognized *L. fulva* but misunderstood the species. Hodgson (1953) keyed *L. fulva* among the smooth-leaved species, and in 1967 (p. 187) she stated "there is no sign of papillae." Also, Hodgson (1962) listed the type locality as Australia, rather than the correct provenance, Auckland Island.

3) The perianth sides are often infolded, particularly in older perianths; this undoubtedly explains the mention of "compresso bilabiato" for the perianth by Hooker and Taylor (1844).

4) Nearly all specimens from New Zealand (excluding Auckland and Campbell Islands) labeled *Lophocolea leucophylla* and determined by Allison, Hodgson or Child are actually either *Chiloscyphus mittenianus* (pp. maj.), *C. aculeatus*, *C. tuberculatus*, or *C. spinifer*.

Notes on Type Specimens—1) *Lophocolea verrucosa* Steph. See Engel (1991d).

2) *Lophocolea fulva* Steph. The specimen represents the suboptimal extreme of the species (see above discussion). The dorsal leaf margin is entire or 1-dentate and the ventral 1–2-dentate or occasionally entire. Leaf apices range from retuse-bidentate to short bifid and have a uniseriate row of the lobe tips composed of (2)3–4(5) cells. However, some shoot sectors, particularly near shoot tips, have undivided and entire leaf apices; this is unique to the species. The specimen has leaf tuberculae typical of the species and exclusively lateral-intercalary branching.

Distribution and Ecology—Campbell, Auckland and Stewart Islands, Tasmania (sea level–1370 m).

The species is one of the more common bryophytes in Tasmania, where it has a rather broad ecological amplitude. It frequently grows in forests of various types, especially in sectors of the island receiving moderate to heavy rainfall. It occurs on rotted, often decorticated, bryophyte-covered logs, where it may form thick, large masses. It is common over litter of the forest floor, sometimes protected by a scrubby cover. It also occurs on peaty mats over damp rocks at stream sides where it may form large, extensive masses, and on damp rocks of roadside banks.

The species occurs in a variety of subalpine niches in Tasmania and in certain areas it is exceedingly common. In subalpine sites it occurs on sloping, wet boulder faces, soil of channels between boulders and on the sides of rills or creek banks. It rather commonly grows over humus under protective scrub cover, and in such situations it may form thick, nearly pure populations. The species also occurs in more exposed niches such as among *Astelia* leaves, as well as on slopes near drainage areas, and then it is associated with *Astelia*, *Drosera*, *Sphagnum*, and others.

On Stewart Is. in a protected niche at the side of a bryophyte covered mound at the summit area of Mt. Rocky (530 m) in mosaic communities of dense heath-forming shrubs to 3 m tall, subalpine herbs, and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma*. Also at Pryse Peak (plateau area on western side of summit, South West Arm, 330–340 m) plants occurred at the side of a bryophyte cushion in an open forest that included stunted *Dacrydium cupressinum*, *Podocarpus hallii*, *Olearia colensoi*, *Gahnia*, *Blechnum*, and bryophyte cushions on the forest floor.

Specimens Seen (selected)—**CAMPBELL IS.:** Garden Cove, *1960 Expedition s.n.*–c. ♂ (CHR); Beeman Hill, ca. 75 m, *1958–59 Expedition s.n.* (CHR); Lyall-Beeman area, ca. 90 m, *Meurk s.n.* (CHR). **AUCKLAND IS.:** *Krong s.n.* (M); *Johnson s.n.* (AK); *Kirk 472* (CHR); Enderby Creek, *Fineran 1612*–c. sporo. (CHR). **NEW ZEALAND. STEWART ISLAND:** Tin Range, *Schuster s.n.*–c. ♂ (CHR); Mt. Rocky summit area, 530 m, *Engel, von Konrat & Braggins 24319* (F); track to Mason's Bay, ca. 1–1.8 km W of Freshwater Hut/Landing, 5 m, *Engel, von Konrat & Braggins 24387*–c. ♂ (F); Pryse Peak, plateau area on western side of summit, South West Arm, 330–340 m, *Engel, von Konrat & Braggins 24677* (F). **TASMANIA.** W facing slope of Mt. Arthur, Pipers River, NE of Launceston and SSE of Lilydale, 850 m, *Engel 15399* (F); Adamsons Peak, *Rodway s.n.* as *L. verrucosa* (HO); ibid., *Weymouth 1425* as *L. verrucosa* (HO); ibid., summit, ca. 1220 m, *Ratkowsky 78/119* (HO); Hartz Mtn. Natl. Park, ca. 700 m, *Hoogland 11734* (HO); ibid., *Ratkowsky H 1363*–c. sporo. (HO); ibid., Mt. Hartz plateau, *Rodway s.n.* as *L. verrucosa*, *s.n.*–c. per. (HO); ibid., summit area of Hartz Peak, 1245–1255 m, *Engel 19885* (F); ibid., ibid., *Ratkowsky 78/132* (HO); ibid., Devils Backbone, above Lake Perry and Lake Osborne, 960–1020 m, *Engel 12813* (F); ibid., summit of Devils Backbone, above Lake Perry and Lake Osborne, 1035 m, *Engel 12835*–c. ♂ (F); along Old Hartz Trail, about 1 mi. beyond Kermandie Plains, ca. 650 m, *Norris 29671* (F); ibid., about 2 mi. W of North Creek, ca. 300 m, *Norris 29519* (F); Huon River, near Tahune Picnic Area, ca. 50–100 m, *Norris 26745* (F); Millhouses Hills, Huon Road, *Weymouth 92* as *L. verrucosa*–c. per. + sporo. (F, HO); Snug River, *Rodway s.n.* as *L. verrucosa* (HO); Mt. Wellington, ca. 425 m, *Rodway s.n.* as *L. verrucosa* (HO); ibid., S facing slope, off Pipeline Track, stream course SE of St. Crispins Well, 640–650 m, *Engel 20192* (F); ibid., St. Crispin's, ca. 610 m, *Weymouth 502* as *L. verrucosa*–c. sporo. (F, HO), *1666* as *L. mooreana*–c. per + ♂ (G), *503* as *L. verrucosa*–c. ♂ + old per. + sporo., *1170* as *L. verrucosa* (HO); ibid., Deep Creek, *Weymouth 281* as *L. verrucosa* (HO); Mt. Field Natl. Park, *Ratkowsky 78/122* (HO); ibid., Beatties Tarn, 975 m, *Engel 14518*–c. ♂ (F); ibid., vicinity of track to Lake Seal, near track entrance to Platypus Tarn, 1050 m, *Engel 14436*–c. ♂ (F); ibid., SE end of Lake Fenton, off Lake Dobson Road, 1020 m, *Engel 13230* (F); ibid., shores of Lake Dobson, ca. 1000 m, *Norris 27628* (F); ibid., Rodway Range, between Rodway Ski Tow and K Col area, 1240–1310 m, *Engel 14391*–c. ♂ (F); ibid., stream above and draining into S end of Lake Seal, E of Rodway Range, 1100–1150 m, *Engel 14348* (F); ibid., Lake Belton, *Ratkowsky H 1362* (HO); ibid., Lake Belcher, *Rodway s.n.* (HO); ibid., Mt. Field, ca. 1065 m, *Rodway s.n.* as *L. verrucosa* (HO); track to Lake Judd, S of Mt. Eliza, E of Lake Pedder, 520 m, *Engel 13738* (F); plateau region E and SE of Mt. Eliza summit, E of Lake Pedder, ca. 1225 m, *Engel 13711*–c. ♂ (F); near Scotts Peak Road, 2.2 km S of junction with Gordon River Road, E of end of Lake Gordon, 580 m, *Engel 13787*–c. sporo. + ♂ (F); Florentine River, near Gordon River Road, 1 km W of junction with Scotts Peak Road, E of S end of Lake Gordon, 380 m, *Engel 15091*–c. ♂ (F); on track to Adamsfield, 2 mi. N of Strathgordon Road, *Norris 33201* (F); Clear Hill Road, 0.9–9.2 km N of Gordon River Road on E side of Lake Gordon, 350–425 m, *Engel 16701* (F); Mt. Tim Shea, *Ratkowsky H 1358* (HO); ibid., 800–900 m, *Ratkowsky 78/123* (HO); Mt. Wedge, 800 m, *Ratkowsky 78/120* (HO); upper reaches of S

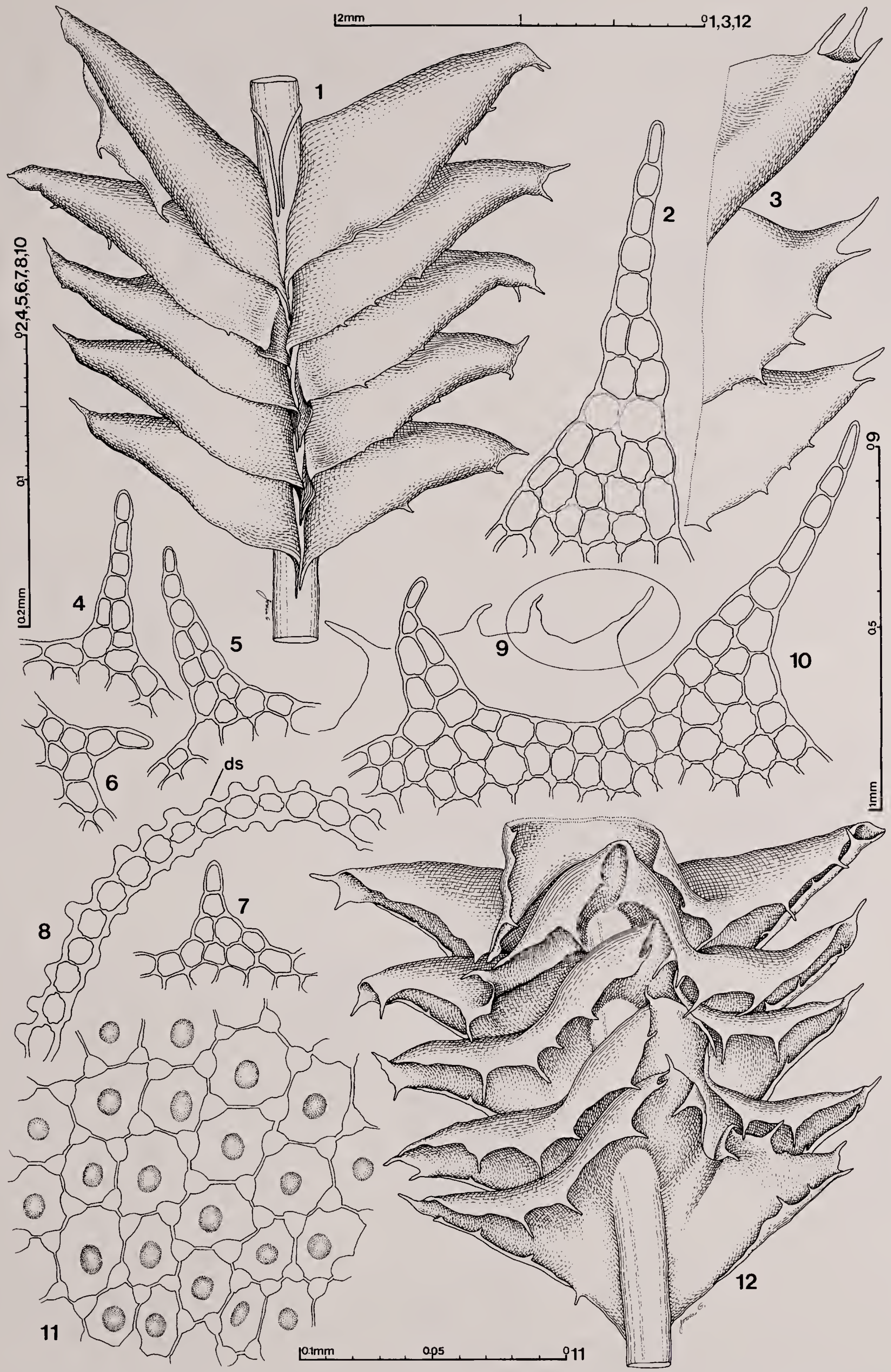

FIG. 64. *Chiloscyphus leucophyllus* (Hook. f. & Tayl.) Gottsche, Lindenb. & Nees. **1.** Shoot, dorsal view. **2.** Ventral segment of leaf. **3.** Distal portion of three leaves from one side of shoot. **4–7.** Teeth of dorsal margin of leaf (all from a single leaf). **8.** Leaf, cross section (ds = dorsal surface). **9.** Underleaf, outline of distal portion. **10.** Portion of underleaf apex (indicated in **9**). **11.** Median leaf cells showing tuberculae. **12.** Shoot, ventral view (rhizoids omitted). (All from type of *Jungermannia leucophylla* [FH].)

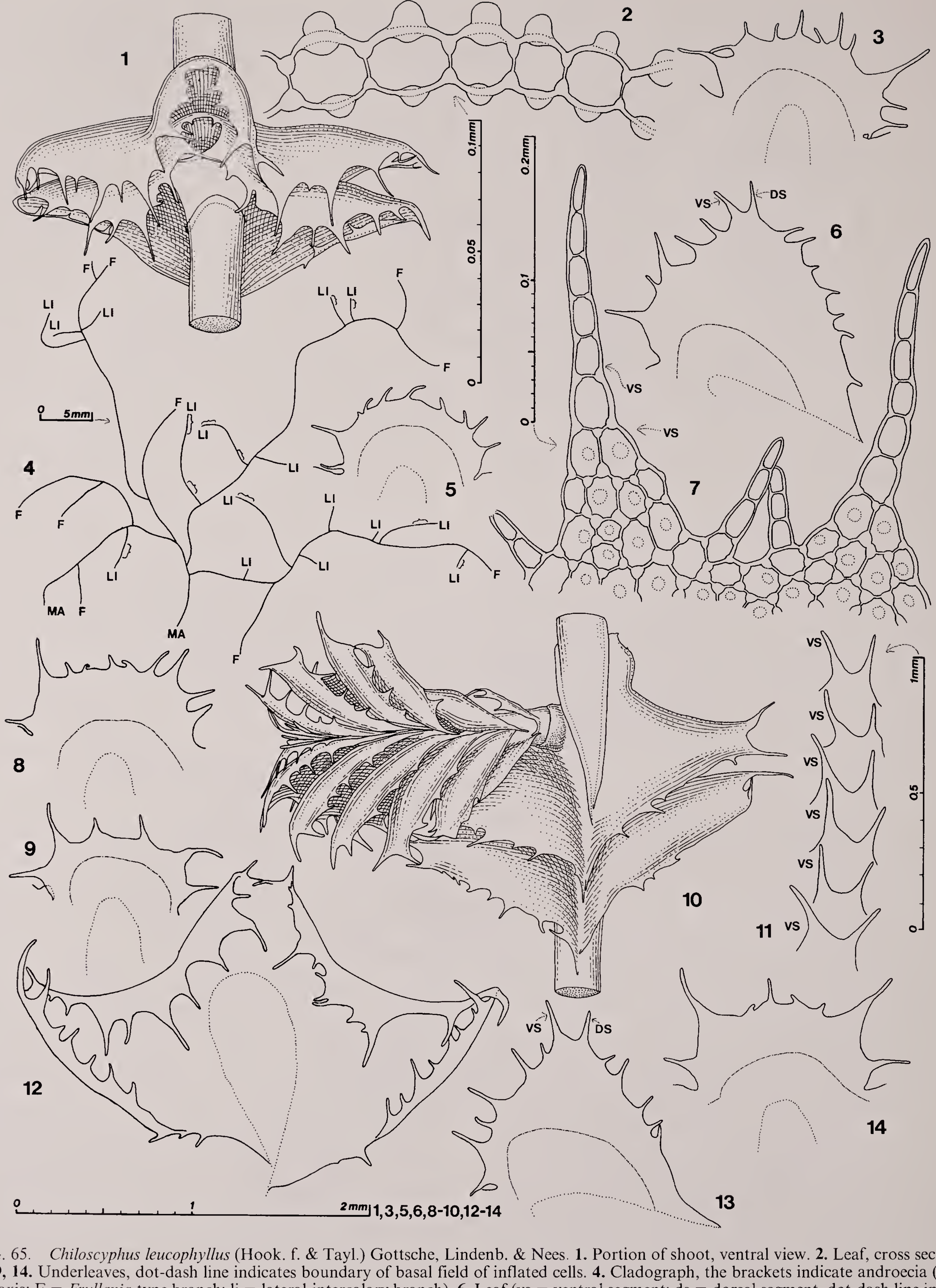

FIG. 65. *Chiloscyphus leucophyllus* (Hook. f. & Tayl.) Gottsche, Lindenb. & Nees. **1.** Portion of shoot, ventral view. **2.** Leaf, cross section. **3, 5, 8, 9, 14.** Underleaves, dot-dash line indicates boundary of basal field of inflated cells. **4.** Cladograph, the brackets indicate androecia (MA = main axis; F = *Frullania*-type branch; li = lateral-intercalary branch). **6.** Leaf (vs = ventral segment; ds = dorsal segment, dot-dash line indicates boundary of basal field of inflated cells). **7.** Leaf apex (vs = ventral segment). **10.** Portion of shoot with lateral-intercalary branch. **11.** Leaf apices, ventral segment (= vs) to left in all figures. **12.** Leaf pair and underleaf. **13.** Leaf (vs, ds, and dot-dash as in **6**). (All figures from *Engel 13787*, Tasmania, near Scotts Peak Road.)

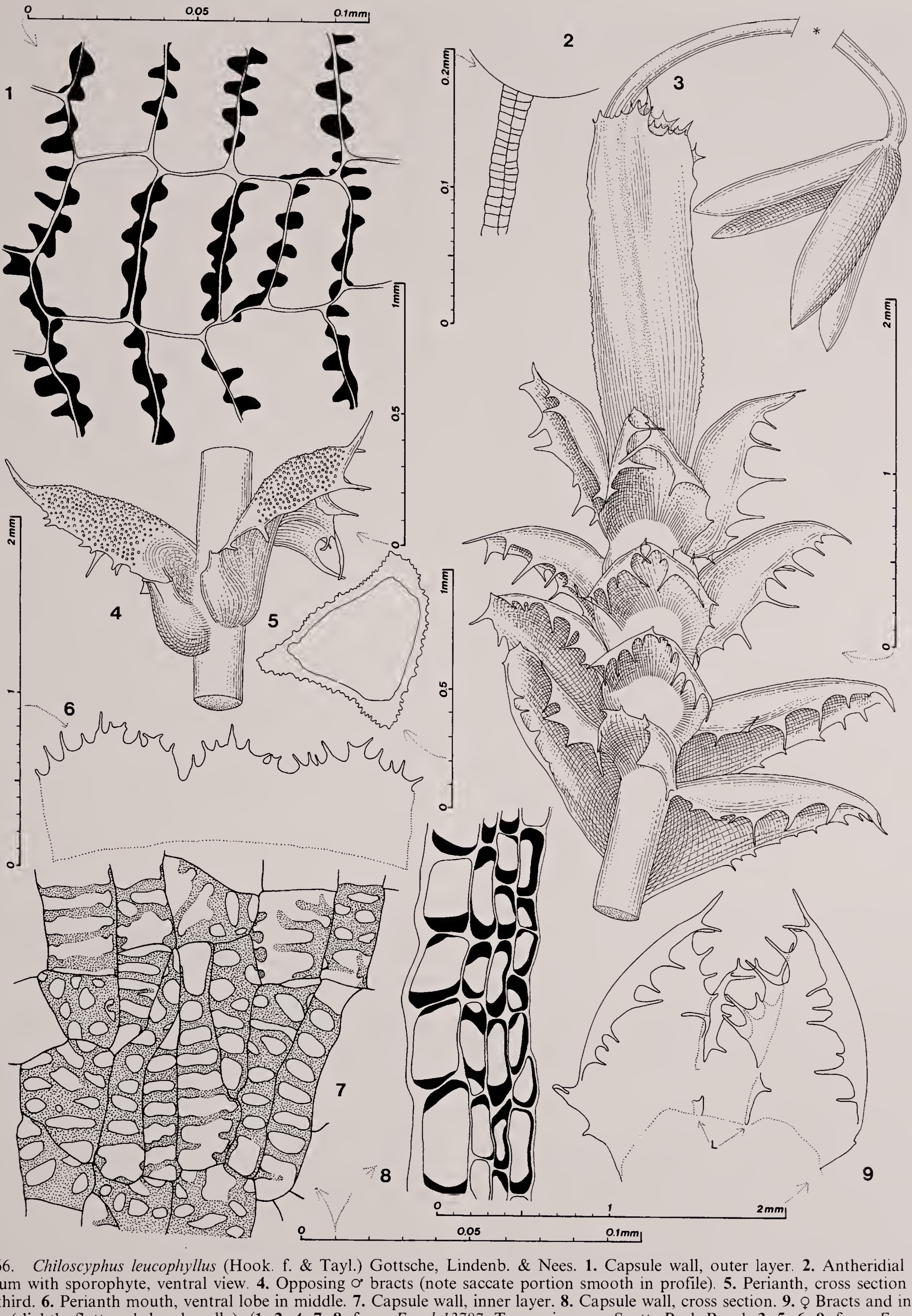

FIG. 66. *Chiloscyphus leucophyllus* (Hook. f. & Tayl.) Gottsche, Lindenb. & Nees. **1.** Capsule wall, outer layer. **2.** Antheridial stalk. **3.** Gynoecium with sporophyte, ventral view. **4.** Opposing ♂ bracts (note saccate portion smooth in profile). **5.** Perianth, cross section through median third. **6.** Perianth mouth, ventral lobe in middle. **7.** Capsule wall, inner layer. **8.** Capsule wall, cross section. **9.** ♀ Bracts and in middle, bracteole (slightly flattened; l = lamella). (**1, 2, 4, 7, 8,** from *Engel 13787*, Tasmania, near Scotts Peak Road; **3, 5, 6, 9,** from *Engel 14878*, Tasmania, King River.)

facing slope of Sentinel Range, between Lake Gordon and Lake Pedder, 700 m, *Engel 15166* (F); Gordon River, just E of confluence with Serpentine River, WNW of Strathgordon 350 m, *Engel 13860*–c. ♂ (F); ibid., vicinity of Sir John Fall, just up river from Butler Creek, ca. 50 m, *Engel 14710*–c. ♂ (F); ibid., Expectation Reach, between Horseshoe Bend and abandoned HEC hut, sea level–50 m, *Engel 14816*–c. sporo. (F); Acheron River, *Gunn s.n.* (BM); Cradle Mtn.–Lake St. Clair Natl. Park, Mt. Rufus, 900–1000 m, *Ratkowsky 78/121* (HO); ibid., Lake St. Clair area, S facing slope in valley between Mt. Rufus and Mt. Hugel, 1120–1130 m, *Engel 19344*–c. ♂ (F); ibid., Mt. Hugel, *Ratkowsky H 1366* (HO); ibid., Lake St. Clair area, plateau ENE of Mt. Rufus summit, 1360–1370 m, *Engel 19412* (F); ibid., Mt. Rufus Circular Track, *Ratkowsky 78/151* (HO); ibid., Pine Valley, Cephissus Falls, NNW of Lake St. Clair, 850 m, *Engel 14266*–c. ♂ (F); Mt. King William I, 1200 m, *Ratkowsky 77/146* (HO); Griffith Creek (tributary of Surprise River), ESE of Mt. Arrowsmith, 1.7 km via Lyell Highway W of King William Saddle and 17.4 km W of Derwent Bridge, 700–720 m, *Engel 19466* (F); upper Surprise Valley, along Lyell Highway between Derwent Bridge and Queenstown, near Camp Creek, 670–730 m, *Schuster 50421a*–c. per. + ♂ (F); Mt. Arrowsmith, S side, along Lyell Highway, 2.7 mi. W of King William Saddle, ca. 610 m, *Schuster 50382*–c. sporo. + ♂ (F); Surprise Valley, along Lyell Highway, 2.7 mi. W of King William Divide, W of Derwent Bridge, near Camp Creek, *Schuster 50367c* (F); Macquarie Harbour, Moore's Track, ca. 45 m, *Moore s.n.* as *L. mooreana* (G, M); Kelly Basin Road (Crotty Track), between junction with Franklin River Road and Kelly Basin, above Nora River, 90 m, *Engel 14959*–c. ♂ + per. (F); ibid., 28.8 km S of Lyell Highway, SSE of Queenstown, 250 m, *Engel 14568*–c. ♂ (F); ibid., 26.9 km S of Lyell Highway, SSE of Queenstown, 250 m, *Engel 14535* (F); Allans Creek, NE slope of Mt. Darwin, off Kelly Basin Road (Crotty Track), 410 m, *Engel 16580* (F); West Coast Range, Proprietary Peak, just N of Mt. Jukes, 1065–1090 m, *Engel 20055* (F); Rinadeena, *Weymouth 906* as *L. verrucosa* (HO); King River, 11.5–12 km by road from Regata Point and 13.5–14 km from Strahan Harbour, sea level, *Engel 14878*–c. sporo. (F); Dubbilbarril, *Weymouth 1106*–c. ♂, *1110* (HO); ibid., King River, ca. 15 m, *Weymouth 988* as *L. verrucosa*, *1085* (HO); ibid., ibid., Mt. Lyell railway, *Weymouth 962* as *L. echinellus* (HO); ibid., King River Gorge, ca. 45 m, *Weymouth 1457* as *L. verrucosa* (F, HO); near Strahan, *Rodway s.n.* (HO); Zeehan, *Rodway s.n.*–c. sporo. (HO); ibid., ca. 60 m, *Weymouth 1488* (HO); road between Zeehan and Trial Harbour, 240–250 m, *Engel 19984* (F); 1 mi. beyond end of Dundas Road, ca. 400 m, *Norris 31323* (F); along road from Melba Flats to Confidence Saddle, 200–400 m, *Norris 31593* (F); Williamsford, ca. 305 m, *Weymouth 1025* (F, HO); ibid., near Mt. Read, *Weymouth 998* as *L. verrucosa*–c. old per. + sporo. (HO); Mt. Read, S of Rosebery, 990–1010 m, *Engel 20026* (F); Cradle Mtn.–Lake St. Clair Natl. Park, Cradle Mtn. area, vicinity of Kathleen's Pool, S of Crater Lake, 1250 m, *Engel 19640* (F); ibid., Plateau Creek area, between Cradle Plateau and Marions Lookout, NNW of Cradle Mtn., 1250 m, *Engel 13973* (F); ibid., Cradle Mtn. area, Weindorfers Forest, 920–1080 m, *Jarman 88/14* (F); ibid., NE side of Crater Lake, 1040 m, *Engel 14060* (F); ibid., Cradle Mtn. area, Hounslow Heath, 1075–1090 m, *Engel 19555* (F); ibid., Pencil Pine, near Cradle Mtn., *Rodway s.n.* (HO); ridge SE of Black Bluff near junction of access road to plateau area and road to Devonport gold mines, S of Burnie, 1000 m, *Engel 16266* (F); Paddys Lake, below and E of Black Bluff, SW of Nietta, 1090 m, *Engel 19775* (F); immediately below summit of Black Bluff, SW of Nietta, 1320 m, *Engel 19829* (F); SE side of Wandle River, where it is crossed by the Murchison Highway, 580 m, *Rowlatt 57B* (F).

Chiloscyphus connatifolius J. J. Engel

> *Chiloscyphus connatifolius* J. J. Engel, Phytologia 83: 42. 1998 (1997). Holotype: Tasmania, Gordon River, Gorge Creek, near Pine Landing, sea level, *Engel 14648* (F); isotype: (HO).

Plants distinctly anisophyllous, rather flexuous, loosely creeping, pale yellow brown in herb., distinctly nitid when dry; shoots medium, 2.6–3.4 mm wide; dried plants with leaves appearing distant and with the distal portion strongly convex to ± terete due to strongly revolute margins. Branches common, mostly of lateral-intercalary type, sporadically of *Frullania* type (the half-leaf with same basic shape as normal leaves). Stems 9–11 cells high, the cortex moderately differentiated (esp. ventrally), in 1–2 layers of smaller, slightly thick-walled cells, the medullary cells increasing in size toward axis middle. Rhizoids short, in tight fascicles from stem at immediate base of underleaves, the tips sometimes digitate. Leaves opposite, horizontal, the shoot flat in dorsal view, the leaves spreading at right angles or nearly so, loosely imbricate, connate dorsally, the orientation strongly succubous, not recurved at ventral end, the leaf arrangement nearly covering the stem in dorsal view except for very narrow strips. Leaves broadly and strongly convex (dorsal view), but not canaliculate distally, subsymmetrically trapezoid, conspicuously widest at the base, the ventral-basal portion of leaf sporadically weakly dilated; apex a- to subsymmetrically bifid to 0.1, the lobes parallel to rather strongly diverging, plane to slightly ventrally sulcate, the ventral commonly larger than the dorsal, the dorsal lobe sometimes basal in juxtaposition to the ventral lobe but never consistently strongly so and never absent altogether, the lobes sporadically subequal; lobes narrowly acute (especially the dorsal) to acuminate, the ventral terminating in a uniseriate row of 2–4 isodiametric to at most moderately elongated cells (1–1.4:1) with thickened exposed walls; dorsal margin straight distally but broadly and slightly curved inward toward base, plane to slightly reflexed, entire, conspicuously long decurrent; ventral margin plane to sharply and abruptly reflexed, the margin + armature mostly aligned toward shoot apex or if aligned ventrally, then revealing at most a short narrow strip of dorsal surface of leaf in ventral view, if ventral margin aligned toward shoot base, then never consistently or strongly so; ventral margin entire or with 1–2 sharp teeth in apical, median or basal sector of margin. Lamina often locally bordered by 1(2) rows of longer and often narrower cells, the border sometimes ill-defined. Cells of leaf on their dorsal and ventral surfaces each with a rather large, domelike, prominent, hyaline tubercle; tuberculae absent on the distal portion of lobes, the median-basal and ventral-basal leaf sectors, the connation sectors, and the underleaves; leaf cells with walls thin, trigones knot-like, median leaf cells 24–36 μm wide, 30–46 μm long. Cells of underleaf + connation tissue + ventral-basal and median-basal sectors of leaf enlarged and with trigones similar to those of median cells. Underleaves much smaller than leaves, *in situ* 1.7–2.3(2.5)× stem width, very wide connate on both sides, the leaf–underleaf juncture distinct when underleaf margins ± parallel with stem, the juncture ill-defined when underleaf margins form a ca. 45° angle with stem, the underleaf margin + basal sector of ventral margin then forming a straight line, the underleaf insertion inverted shallowly U-shaped, the underleaves slightly to moderately spreading, contiguous to locally loosely imbricate, slightly concave (ventral view), quadrate to subtrapezoid when flattened; apex broadly rounded, bidentate to more often bilobed to 0.3–0.45, the lobes narrowly acute to subacuminate, always exceeding magnitude of any other underleaf armature, terminating in a single cell or a uniseriate row of 2–3 elongate cells, the apex otherwise lacking other armature; lamina margins plane to slightly recurved, on each side with a cilium or broad-based tooth in median or distal sector, the marginal armature always basal to the main lobes and clearly marginal in position (the underleaves therefore never 4-lobed), the margins occasionally with an accessory tooth basal to the main lateral armature. Asexual reproduction absent.

Plants dioecious. Androecia subfoliose grading to subspicate, on main shoot or rather long lateral-intercalary

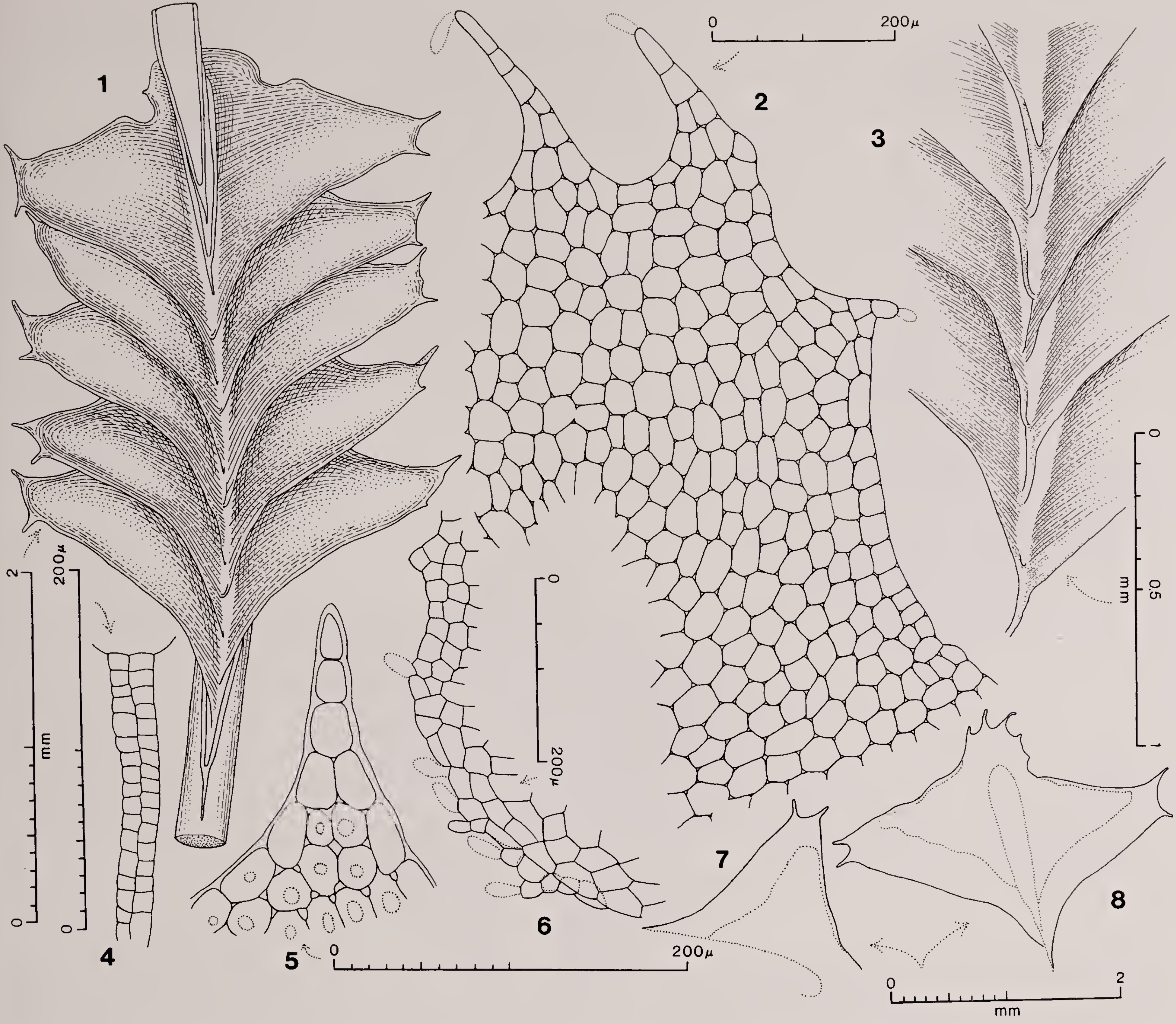

FIG. 67. *Chiloscyphus connatifolius* J. J. Engel. **1.** Sector of main shoot, dorsal view. **2.** Lateral half of underleaf and associated connation tissue. **3.** Sector of main shoot showing details of leaf connation. **4.** Antheridial stalk. **5.** Ventral segment of leaf. **6.** ♂ Bract lobule margin. **7.** Leaf, the sector of inflated cells within stippled line. **8.** Two leaves and attached underleaf, the sector of inflated cells within stippled line. (All from *Engel 14648*, Tasmania, Gordon River.)

branches, sporadically on rather long *Frullania*-type branches, the androecia initially terminal but eventually become intercalary, sometimes long, with to 12 pairs of bracts per androecium. Bracts moderately to distinctly smaller than leaves, strongly dorsally assurgent throughout and then subvertical, or, more often, the basal, saccate portion dorsally assurgent and the distal portion reflexed, obliquely spreading, and subhorizontally oriented, the bracts closely imbricate, the saccate portion fused at base with opposite bract and crenulate in profile by bulging convex-sided cells, the dorsal-basal portion distinctly ventricose, the apex usually bidentate-bilobed, occasionally 1-lobed or undivided; lobule margin inflexed to involute, irregularly crenulate-denticulate and with numerous slime papillae; antheridia solitary, the stalk biseriate. Gynoecia with a plagiochiloid appearance (particularly when immature) in dorsal view, subisophyllous, on main shoot or rather long lateral-intercalary branches, occasionally on long *Frullania*-type branches; subfloral innovations lacking; vestigial stem perigynium present, the bracts and bracteoles of innermost and second series inserted on the vestigial perigynium. Bracts of innermost series considerably larger than leaves, erect and ensheathing the vestigial perigynium and lower sector of perianth, falcate-ventrally secund, distinctly connate dorsally, convex toward base, the distal portion ± canaliculate, the bracts ovate, distinctly narrowed toward apex, subsymmetrically to strongly asymmetrically bifid: the ventral lobe slightly to markedly larger, apiculate to more often acuminate, the dorsal narrowly acute to subacuminate, often distinctly basal in juxtaposition to the ventral lobe, the margins of both lobes entire, the margin defining sinus base occasionally with a small sharp tooth; dorsal margin of lamina undulate, sharply reflexed, entire; ventral margin strongly reflexed, entire or with 1–2 small teeth in distal half. Bracteoles of innermost series smaller than

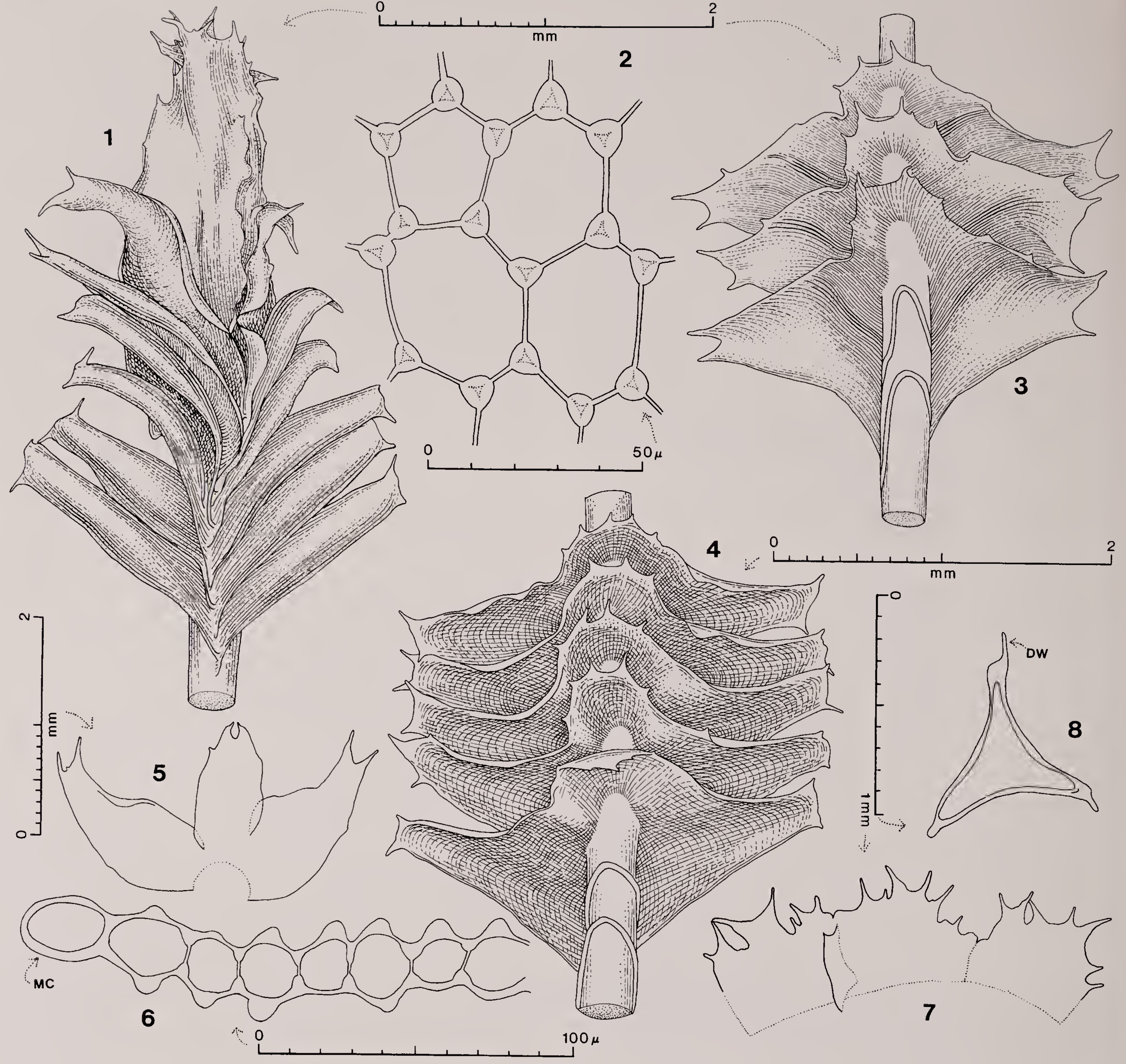

FIG. 68. *Chiloscyphus connatifolius* J. J. Engel. **1.** Gynoecium, dorsal view; note connation of bracts. **2.** Median leaf cells. **3, 4.** Sectors of 2 different main shoots, ventral view. **5.** ♀ Bracts and in middle, bracteole. **6.** Leaf, cross section (mc = marginal cell). **7.** Perianth, cross section through median sector (dw = dorsal wing). **8.** Perianth mouth, ventral lobe in middle. (All from *Engel 14648*, Tasmania, Gordon River.)

bracts, ca. 0.6–0.65 area of bracts, connate on both sides, but more narrowly so on one side, sometimes very broadly connate on both sides, concave (ventral view), elliptic; apices short bifid, the lobes ventrally sulcate, apiculate; lamina margins entire or 1–2-dentate. Bracts with small tuberculate cells distally, and with a large field of inflated smooth or tuberculate cells toward base, the bracteole cells smooth throughout or with a small field of tuberculate cells distally. Perianth longly exserted beyond bracts, sharply trigonous throughout, the sides often infolded, the perianths narrowly elliptic, slightly narrowing toward the wide, shallowly 3-lobed mouth; lobes undivided to obscurely bifid, the segments, when developed, acuminate, the lobes otherwise spinose dentate-laciniate; keels sharp, with keelar wings common, of several cells high, the dorsal wing broadest, the wings sparingly armed. Perianth cells mostly smooth, but the outer face with local small fields of tuberculate cells, particularly near keels.

Sporophyte not seen.

DIFFERENTIATION—This species combines important features of several species within the *Leucophylli*. The interrelationships of these species with *C. connatifolius*, and with each other, are illustrated in Table 14.

Chiloscyphus connatifolius is most closely related to *C. tuberculatus* and *C. leucophyllus*. With *C. leucophyllus* it

TABLE 14. Comparison of *Chiloscyphus connatifolius* with other taxa (exc. *C. aculeatus*) in sect. *Leucophylli*. LIB = lateral-intercalary branch; F = *Frullania*-type branch.

Character	*C. connatifolius*	*C. tuberculatus*	*C. leucophyllus*	*C. mittenianus*
Branch type frequency [1–4, frequency increases]	F = 2 LI = 4	F = 4 LI = 3	F = 3 LI = 4	F = 4 LI = 2
Armature of dorsal margin of leaf	entire	0–6 processes	3–7(9) spinose-dentate	4–7 processes (except suboptimal variants)
Armature of ventral margin of leaf	entire or with 1–2 sharp teeth	(1)2–4 processes	3–5 processes	processes sparing to copious
Alignment of ventral leaf margin + armature	usually toward shoot apex	toward shoot base or ventral-basal	normally toward shoot base	various, never consistently toward shoot base
No. of cells in uniseriate row of leaf ventral lobe	2–4	(4)5–7	(4)5–7(8)	2–3(4)
Length:width ratio of cells in uniseriate row of leaf lobe	1–1.4:1	1.6–3.3:1	at most slightly elongated	at most slightly elongated
Underleaf width vs. stem width	1.7–2.3(2.5)×	1.1–1.9×	1.8–2.9×	2.8–3.6×
Underleaf apex form	main lobes (2) larger than all other underleaf armature	median pair of processes larger than outermost pair	outermost pair of processes larger than intervening armature	outermost pair of processes larger than intervening armature
Underleaf summit armature	2 lobes only; accessory = lacking	2 or 4 lobes only; accessory = lacking	ciliate or small-dentate between outermost pair of processes	coarsely spinose dentate-laciniate
Underleaf cell tuberculae	absent	present	present	present
Innermost bract margins	entire or with 1–2 small teeth on ventral margin	ciliate to laciniate	spinose dentate-laciniate	spinose dentate-laciniate
Profile of ♂ pocket	crenulate by bulging cells	tuberculate-mamilliform	smooth, at most, with convex cells	smooth
♂ Lobule margin	crenulate-denticulate	2–3-dentate	crenulate	crenulate
Dorsal connation of leaves	connate	free	free	free
Sector of inflated cells of underleaf	throughout underleaf	median-basal field	median-basal field	median-basal field
Shoot width (mm wide)	2.6–3.4	0.75–1.2	1.5–2.4 mm	to 3.8 mm
Distribution	Tasmania	New Zealand (South Is.)	Tasmania + Auckland and Campbell Is.	New Zealand, Auckland, and Campbell Is.

shares: 1) branching modalities; 2) at most moderately elongated cells of the leaf lobe uniseriate row; and 3) similar underleaf width vs. stem width. However, underleaf characters are fundamentally different from *C. leucophyllus* and more like those of *C. tuberculatus*. The underleaf summit of *C. connatifolius* is bidentate or, more often, bilobed, while the margins on each side have a cilium or tooth-like process (never laciniiform like *C. leucophyllus*) situated in the median or distal sector at a position always basal to the two primary lobes at the apex (Fig. 67: 2, 8). Like *C. tuberculatus* the underleaf summit of *C. connatifolius* has no armature other than the lobes.

NOTE—Leaves are variously connate dorsally. Connation basically involves the tip of the decurrent strip of a leaf with the dorsal-basal surface of the opposing leaf (Fig. 67: 1, 3). The decurrent strip of the lowermost leaf of the opposing pair often in turn fuses with the dorsal-basal surface of the leaf opposing that strip (Fig. 67: 3). Fusion only occasionally involves solely the extremities of opposing dorsal leaf bases.

DISTRIBUTION AND ECOLOGY—The species is known only from a few sites in Tasmania: one in the southeast (Geeveston), the others in the western sector (along the Gordon River). It occurs at sea level on boulders of stream banks where some soil has accumulated; it may be mixed with *Chiloscyphus novaezeelandiae*.

SPECIMENS SEEN—**TASMANIA.** Geeveston, *Rodway s.n.* as *L. leucophylla*–c. ♂ (HO); Gordon River, Sir John Falls, just up river from Butler Is., sea level, *Engel 14695B* (F).

Chiloscyphus mittenianus (Colenso) J. J. Engel

Isotachis mitteniana Colenso, Trans. & Proc. New Zealand Inst. 21: 69. 1889 (1888). *Chiloscyphus mittenianus* (Colenso) J. J. Engel, Bryologist 94: 312. 1991. Lectotype (*fide* Engel, 1991d) New Zealand, North Is., Waipawa Co., "Ourisia slip, Redclyffe River," i.e., near Norsewood, 1885, *Colenso a. 1300* (WELT!–c. sporo.); isolectotype: (BM!–c. sporo.).

Plants subisophyllous, rather stiff, ascending to suberect to erect, if on a steep incline, then appearing negatively geotropic, pale green to pale yellow green, the older sectors often olive green to yellow brown, the tips often whitish green, distinctly nitid when dry; shoots rather large, to 3.8 mm wide, sometimes becoming very long, such as to 10 cm long; dried plants with distal portion of leaves appearing ± terete due to strongly revolute margins. Branches common, mostly of *Frullania* type (the half-leaf of similar shape to vegetative leaves), the branches sporadically of lateral-intercalary type (originating dorsal to leaf–underleaf connation). Stems smooth, 16–18 cells high, the cortex well differentiated (especially dorsally), in 2–3 layers of distinctly thick-walled cells; medullary cells thin walled. Rhizoids in tight, cylindrical fascicles from stem at immediate base of underleaves, the tips sometimes digitate. Leaves subopposite, the dorsal sector subhorizontal to nearly perfectly horizontal (except sometimes at extreme base, which may be dorsally assurgent), the shoot thereby appearing distinctly flat in dorsal view, the leaves distinctly widely spreading, imbricate, free dorsally, the orientation strongly succubous, the insertion slightly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement practically covering the stem in dorsal view except for very narrow V-shaped sectors. Leaves broadly and strongly convex (dorsal view), the distal portion of leaf strongly convex to canaliculate (best observed in ventral view), the distal portion sometimes only slightly convex in suboptimal plants, rarely plane; leaves asymmetrically deltoid, conspicuously widest at the base, the ventral-basal portion of leaf conspicuously dilated and broadly rounded-subauriculate, the leaf subsequently abruptly narrowing distally, the median portion ventrally forming a concave line which may define a shallow "sinus;" apex with ventral lobe much larger than the dorsal, the dorsal lobe usually reduced to a tooth distinctly basal in juxtaposition to the ventral lobe, the dorsal lobe sometimes absent altogether; morphological ventral lobe narrow to medium acute to acuminate, sometimes apiculate, terminating in a uniseriate row of 2–3(4, very rarely and inconsistently 5) at most slightly elongated cells; apex sporadically narrowly rounded and entire (var. *obtusus*) or, very rarely, symmetrically short bifid and with lobes subequal, piliferous and with the ventral terminating in a uniseriate row of 5–7(8) cells (var. *symmetricus*); dorsal margin nearly straight to broadly and gently curved, plane toward base but abruptly reflexed to subrevolute distally, 4–7-spinose dentate, rarely entire; ventral margin with dilated sector plane to broadly reflexed, the distal portion strongly reflexed, the ventral margin variously oriented but never consistently oriented toward shoot base; ventral margin sparingly to copiously spinose dentate-laciniate, particularly on the dilated portion. Leaf cells on their dorsal and ventral surfaces (and cells of both surfaces of underleaf) each with a rather small, domelike, prominent, hyaline tubercle which collectively glisten in leaf profile; tuberculae absent on distal part of lobes, marginal armature and some median-basal inflated cells; leaf cells with walls thin, trigones large to knot-like, median leaf cells 32–44 μm wide and long; leaves and underleaves with a median-basal field of inflated cells with smaller trigones. Oil-bodies (3)5–7 per cell, finely botryoidal, but the segmentation ill-defined, the oil-bodies rapidly breaking up. Underleaves of well-developed plants strikingly similar in appearance to those of *Bazzania involuta*, the distal sector recurved to revolute when dry; underleaves a little smaller than leaves, *in situ* 2.8–3.6× stem width, rather broadly connate on both sides, less often rather narrowly so and rarely very broadly so, sometimes connate more strongly on 1 side than the other; underleaf insertion inverted U-shaped, the underleaves rather strongly spreading, imbricate, concave to subcupulate (ventral view), subquadrate to obtrapezoid, the distal portion broadly reflexed in well-developed plants; apex undivided and truncate to (often) broad lunate, moderately to copiously spinose dentate-laciniate (up to 11 processes, rarely sparsely armed), the outermost processes normally are the largest and probably morphologically represent the lobes, the median armature irregular and smaller, the armature reflexed (ventral view); lamina margins broadly recurved, moderately to rather copiously spinose dentate-laciniate, rarely entire or with a small tooth. Asexual reproduction absent.

Plants dioecious. Androecia usually on main shoots or elongate *Frullania*-type branches, rarely on lateral-intercalary branches, initially terminal but eventually become intercalary, often long, with to 20 pairs of bracts per androecium; bracts of two intergrading types, the first type much more common: 1) subfoliose, the bracts foliaceous, of similar shape and form as vegetative leaves but somewhat smaller, rather strongly dorsally assurgent, widely spreading, succubous to at most subtransverse in orientation and with imbrication much as in vegetative leaves, the bracts of this type tend to occur on main shoot and elongate branches; 2) subspicate, of basic form as vegetative leaves but much smaller, the bracts erect to obliquely spreading, transversely oriented and closely imbricate, the bracts of this type on rather short branches; bracts of both types free dorsally, the dorsal-basal portion distinctly ventricose and smooth in profile. Lobule margin involute, crenulate and with copious slime papillae; antheridia 1(2) per bract, small for bract size, the stalk biseriate. Gynoecia subisophyllous, on main shoot; subfloral innovations sometimes present, from below bracts of third (lowermost) series; vestigial stem perigynium present, the bracts and bracteoles of innermost series inserted on the vestigial perigynium. Bracts of innermost series much larger than leaves in size, erect and ensheathing perianth, free from one another, broadly convex, the distal portion canaliculate, the bracts broad ovate but otherwise with similar basic form of vegetative leaves; lamina margins spinose dentate-laciniate, crispate toward the base, the dorsal margin sharply reflexed, the ventral ± plane. Bracteoles of innermost series somewhat smaller than bracts, ca. 0.65–0.75 bract area, rather broadly connate on both sides, concave (ventral view), subquadrate to broadly subelliptic; apices truncate (sometimes obliquely so), spinose dentate-laciniate; lamina margins spinose dentate-laciniate. Bract and bracteole with small tuberculate cells distally, and with a very large field of inflated cells in basal half. Perianth longly exserted beyond bracts, sharply trigonous for most of its length, the sides often infolded, particularly in older perianths, the perianths narrowly oblong, not narrowing toward the wide, shallowly 3-lobed mouth; lobes undivided and broadly rounded, with low, broad teeth and small laciniae; keels sharp, with keelar wings common, conspicuous and of many cells high, the wings armed with spinose teeth and small laciniae. Perianth cells on both outer and inner surfaces each with a prominent domelike tubercle; cells of apical extremity of perianth smooth, those toward base inflated and smooth. Calyptra small, extending to ca. 0.4–0.6 the perianth length at maturity.

Seta observed only in collapsed state. Capsule 44–48 μm thick, of 6 layers, the outer layer of cells equal to thickness of 3–3.5 of interior strata; outer layer of cells subquadrate to subrectangular (a few long rectangular), the radial walls thin, with red-brown nodular to sporadically spine-like thickenings, the thickenings mostly on longitudinal walls, sporadically on transverse walls, the exposed tangential wall thickened; intermediate layers each thicker than inner layer, the intermediate layers with vertical thickenings often considerably tangentially extended, with semiannular bands absent; innermost layer of cells irregularly quadrate to rather long rectangular, the walls thin, with semiannular bands red brown, rather wide, close and numerous, sometimes nonpigmented in median portion, sporadically incomplete, often forked and anastomosing to delimit fenestrae, the radial walls lacking nodular thickenings.

Spores (11.9)12.4–13.5 µm, thin walled, with faint, dense, low but sharply defined, close, papillose and short-vermiculate markings; spore:elater diameter ratio 1.5–1.8:1. Elaters somewhat tortuous, less often rigid, 7.2–9.1 µm wide, the spirals 1.9–2.4 µm wide.

DIFFERENTIATION–VARIATION—The ventral-basal portion of the leaf is diagnostically dilated and broadly rounded to subauriculate. At the base of this "hump" lies a projection—usually laciniiform—but quite variable in stature. The leaf abruptly narrows immediately distal to this projection, and at that position there is often a concave line which may take the shape of a shallow sinus. Such leaves, *in situ*, sometimes appear to have a different morphology than more typical plants: the leaves appear very broad ovate, with an obliquely truncate apex which is distinctly bifid. In such leaves, the dorsal lobe appears to be the distalmost, strongly convex-canaliculate projection, while the ventral lobe appears to be the above mentioned laciniiform projection at the base of the "hump." The two "lobes" appear to be separated by a sinus and often a spinose tooth or small lacinium. If such leaves are removed and flattened, the actual shape and morphology of the variant are revealed.

In optimal plants, the distal portion of the leaf is strongly concave to canaliculate (ventral view) (Fig. 69: 8). This feature, coupled with the narrow to medium acute apex (which terminates in a cuspidate to apiculate tip) and the dilated ventral-basal portion of the leaf lends a unique aspect. However, somewhat lax plants occasionally have leaf apices slightly concave or even plane. Plants with such leaves may appear quite different upon first examination, and should be treated with care.

A suboptimal, sparsely armed variant initially may be confusing (see Fig. 69: 2). This facies is characterized by 1) underleaves more broadly connate than in optimal plants; 2) underleaf apex for the most part sparsely, or at most moderately, armed; 3) underleaf margins entire or with a small tooth; 4) ventral margin of the leaf sparsely armed; 5) dorsal margin of leaf entire or at most with a few small teeth; and 6) leaf apex for the most part apiculate or, sporadically, merely very narrowly rounded, i.e., without the development of a cusp or angular tip. Examples of this variant are *Engel 18602* and *18694*.

Juvenile or subjuvenile plants at first may be confused with *C. aculeatus*. Such plants have ± the stature of *C. aculeatus*, and have underleaves of some shoot sectors with only four processes. Careful examination will reveal underleaf characters that exclude *C. aculeatus* and place the plant in *C. mittenianus*. For example, underleaves with only four processes have the marginal pair much larger. Moreover, shoots that bear such underleaves also have underleaves more typical of *C. mittenianus*: two prominent processes at the junction of apex and lateral margin and between these occur at least three irregular processes. Original material of *Chiloscyphus vulcanicus* Colenso is such a collection (see Notes on Type Specimens); other examples exist in herbaria as misdeterminations of *C. aculeatus*.

Similar to this suboptimal phase are plants that represent an extreme in reduction of armature. However, this extreme has features that extend beyond the spectrum of variation involving the sparsely armed variant, and it is separated from well-developed and even suboptimal plants by a break in that continuum. In my opinion, the relative taxonomic isolation afforded by differentiation of the extreme (cf. key below) does not extend beyond the limits of *C. mittenianus*. Therefore, I have recognized the extreme phase taxonomically at the varietal level.

Chiloscyphus mittenianus may be divided into three varieties, separable as follows.

Key to Varieties of *C. mittenianus*

1. Leaf apices subequally divided (rare) or appearing sharply angular, varying from medium acute to acuminate, the apices at most only sporadically very narrowly rounded in suboptimal plants (var. *mittenianus*), the ventral lobe slightly to markedly larger than the dorsal; leaves uniformly free dorsally; underleaves uniformly broadly connate on both sides 2
   2. Leaf apices strongly asymmetric: the ventral lobe much larger than the dorsal, which is usually distinctly basal in juxtaposition to the ventral lobe (the dorsal at times absent altogether), the shape of the leaf apex defined by the ventral lobe, which varies from medium acute to apiculate to acuminate; ventral lobe terminating in a uniseriate row of 2–4 cells; plants common . . . . . . var. *mittenianus*
   2. Leaf apices subsymmetric to symmetric: the dorsal lobe not consistently smaller than the ventral and only sporadically slightly basal in juxtaposition to the ventral lobe, with both lobes piliferous; ventral lobe terminating in a uniseriate row of 5–7(8) cells; plants very rare . . . . var. *symmetricus*
1. Leaf apices normally narrowly rounded, rarely and sporadically acute or apiculate; leaves frequently connate dorsally; underleaves occasionally free on 1 side . . . . var. *obtusus*

Chiloscyphus mittenianus (Colenso) J. J. Engel, **var. *mittenianus***

Chiloscyphus vulcanicus Colenso, Trans. & Proc. New Zealand Inst. 21: 59. 1889 (1888) ("*vulcanica*"), *syn. fide* Engel (1991d). Type: New Zealand, North Is., East Taupo Co., Mt. Tongariro, 1887, *Hill* (BM!, WELT!).

Chiloscyphus hispidus Steph., Spec. Hep. 6: 308. 1922, *syn. nov.* Type: New Zealand, South Is., Lake Wakatipu, 1910, *Mecklejohn 216*, ex hb. Lillie (G!).

Leaves uniformly free dorsally; apices with the ventral lobe much larger than the dorsal, which is usually distinctly basal in juxtaposition to the ventral lobe (the dorsal at times lacking altogether), the shape of the leaf apex defined by the ventral lobe, which varies from medium acute to apiculate to acuminate and which terminates in a uniseriate row of 2–3 cells. Underleaves uniformly broadly connate on both sides.

NOTES ON TYPE SPECIMENS—1) *Isotachis mittenianus* Colenso See Engel (1991d).

2) *Chiloscyphus vulcanicus* Colenso. Original specimens at BM and WELT are discussed in Engel (1991d). Some shoot sectors in these specimens (particularly near base) have underleaves with four processes at the summit, and thus bring to mind *C. aculeatus*. However, other sectors have underleaf apices more like the protologue, being retuse and with "long teeth, six at top." Some underleaf apices have more than six processes, but regardless of relative underleaf development,

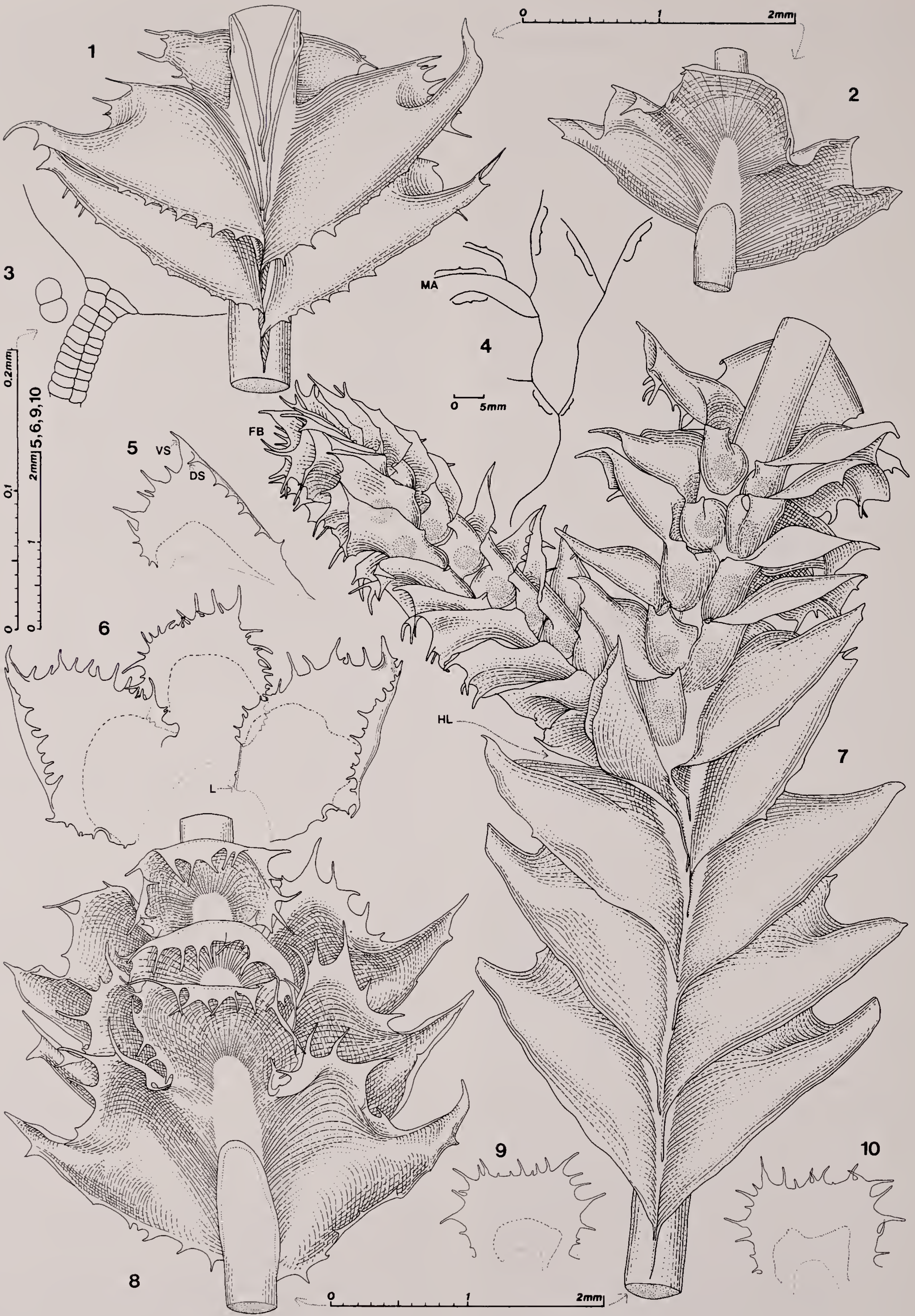

FIG. 69. *Chiloscyphus mittenianus* (Col.) J. J. Engel. **1.** Portion of shoot, dorsal view. **2.** Portion of sparsely armed variant, ventral view. **3.** Antheridial stalk and to left, cross section through stalk. **4.** Cladograph, the brackets indicate androecia; all branches of *Frullania* type (MA = main axis). **5.** Leaf, ventral view (vs = ventral segment; ds = dorsal segment). **6.** ♀ Bracts and in middle, bracteole (l = lamella). **7.** Subfolious androecium on leading shoot and subspicate androecium on *Frullania*-type branch (= FB). (HL = half-leaf). **8.** Portion of shoot, ventral view. **9, 10.** Underleaves. (Dot-dash line in **5, 6, 9, 10** defines basal zone of inflated cells). (**1, 3–5, 7–10,** from *Engel 18861*, New Zealand, South Is., Tutoko River; **2,** from *Engel 18602*, New Zealand, South Is., below Mt. Burns; **6,** from *Schuster 48370*, New Zealand, South Is., ca. 0.5–0.6 mi. from front of Fox Glacier.)

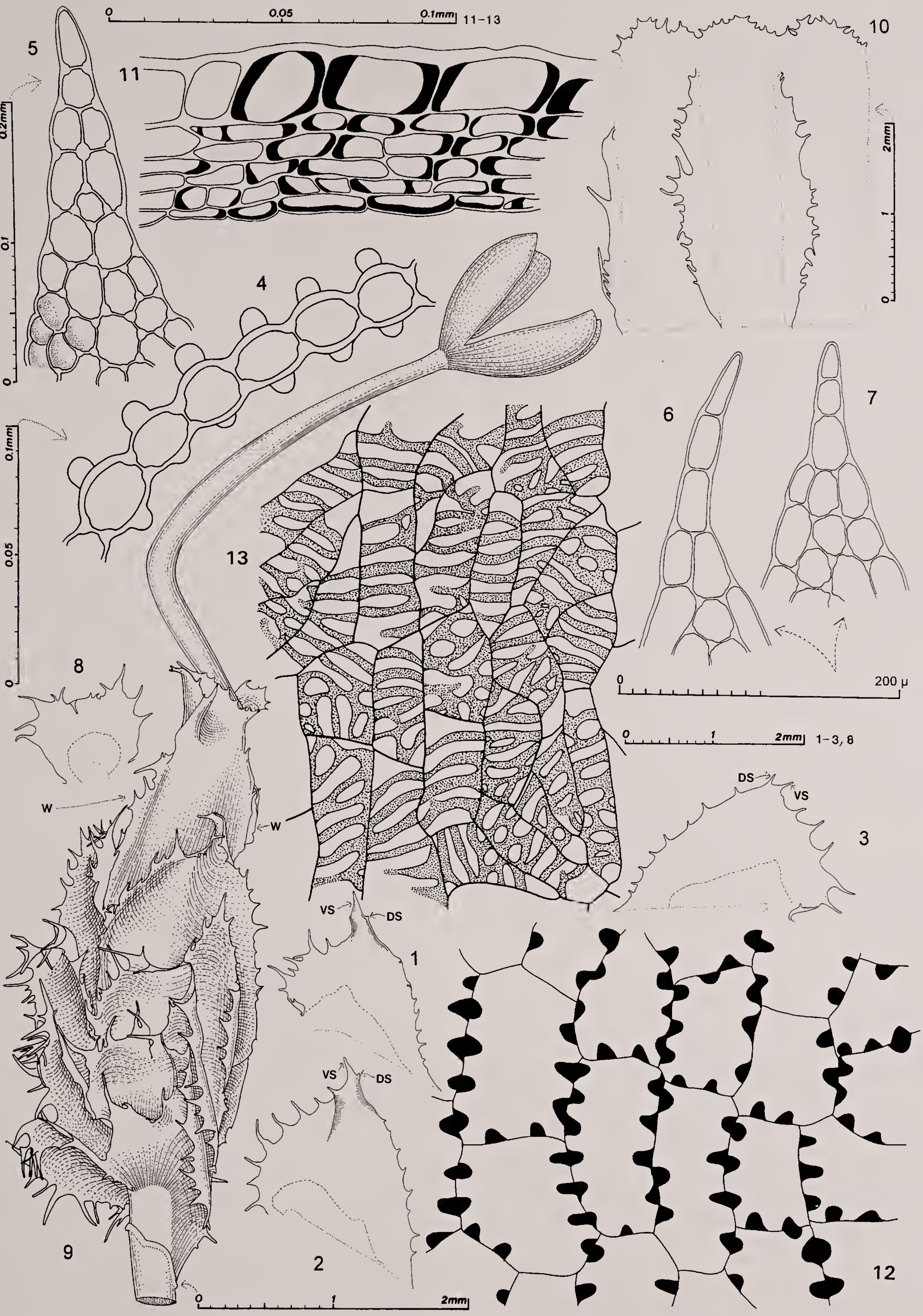

FIG. 70. *Chiloscyphus mittenianus* (Col.) J. J. Engel. **1, 2.** Leaves, ventral and dorsal views, respectively (vs = ventral segment, ds = dorsal segment). **3.** Leaf (flattened; vs = ventral segment, ds = dorsal segment). **4.** Leaf, cross section. **5–7.** Ventral segment of leaf. **8.** Underleaf. **9.** Gynoecium and sporophyte, lateral-ventral view (w = wing). **10.** Perianth, ventral face in middle (note wings). **11.** Capsule wall, cross section. **12.** Capsule wall, outer layer. **13.** Capsule wall, inner layer. (Dot-dash line in **1–3, 8** defines basal zone of inflated cells). (**1, 2, 4, 5, 8,** from *Engel 18861*, New Zealand, South Is., Tutoko River; **3,** from *Engel 17993*, New Zealand, South Is., Otago/Westland Prov. boundary, Mt. Aspiring Natl. Park, summit area of Haast Pass; **6, 7,** from *Engel 18532B*, New Zealand, South Is., Westland/Canterbury Prov. boundary, Arthur's Pass Natl. Park, Upper Twin Creek Valley; **9–13,** from *Schuster 48370*, New Zealand, South Is., ca. 0.5–0.6 mi. from front of Fox Glacier.)

the pair of processes at the juncture, on each side, of apex and lateral margin are uniformly the largest.

3) *Chiloscyphus hispidus* Steph. The specimen consists of somewhat flaccid, androecial plants. Trigones are weakly to distinctly knot-like, but overall smaller than optimal *C. mittenianus*. The reduced trigone stature correlates with the flaccid plant texture.

Distribution and Ecology—This variety occurs on Campbell and Auckland Is. and is widespread in New Zealand (South Is., sea level–1740 m; North Is., 75–1370 m).

Variety *mittenianus* is one of the more common taxa in the genus. It has a broad ecological amplitude, and in a number of different ecological situations forms smaller caespitose tufts or, frequently, extensive ± pure masses. It frequently is present at middle elevations as a component of wet, rich, dense forests as well as less shaded, sometimes quite open areas within the forest or at its edge. It often is terricolous, especially in moist or humid, well-drained sites such as steep slopes (especially those with seepage areas) and damp or wet banks. In such situations it often is associated with a number of other bryophytes, and the forest floor or bank may be quite bryophyte rich. The variety also is rather commonly associated with watercourses, occurring on boulders of stream beds and banks (particularly in niches that have accumulated silt or gravel) and on earth in niches just above watercourse banks, at times among shrubs, at times without such protection. It also occurs on well-shaded, dripping rock faces within forests. The variety is common on roadside banks, especially in niches associated with dripping rock faces that are covered by hepatics and mosses. It is less common on rotted logs or stumps, but on this substrate it appears to be much more prevalent in later stages of bryophyte succession, i.e., as a component of bryophyte-covered logs or stumps.

In subalpine or alpine areas var. *mittenianus* may be found on the sides of rills, on damp soil under shrub or tussock cover, or in boggy areas. For example, at 1400–1480 m in the vicinity of Mt. Robert Skifield (Nelson Lakes Natl. Park, *Engel 22819*), an area of tarns within low alpine vegetation, the variety occurs near tarns in very wet niches between tussock, and is often covered by old dead tussock blades.

Specimens Seen (selected)—**CAMPBELL IS.:** *Sorenson s.n.* (CHR); *Taylor s.n.* as *L. leucophylla* (AK); Beeman, *Roberts s.n.* (AK); near top of Mt. Juma, ca. 490 m, *Taylor 39* (AK); Tucker Cove Valley, *Oliver s.n.* (CHR); E slopes of Mt. Honey, 100 m, *Meurk H8298* (WELT); near summit of Mt. Dumas, ca. 500 m, *Meurk H8308* (WELT) . **AUCKLAND IS.:** Hooker Hills, *Fineran 1768pp* (CHR). **NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Lake Hauroko, ca. 305 m, *Child H 1566* as *L. leucophylla* (F); Fiordland Natl. Park, plateau and slopes below Mt. Burns, E of Borland Saddle, S of South Branch of Borland Burn, W of Monowai, 1225–1320 m, *Engel 18602* (F); ibid., stream valley just SW of Mt. Burns, S of South Branch of Borland Burn, W of Monowai, 1010–1170 m, *Engel 18676* (F); ibid., Mt. Burns, ca. 1280 m, *Child H 5043* (F); ibid., summit of Borland Saddle, off track to Mt. Burns, S of South Branch of Borland Burn, W of Monowai, 1090 m, *Engel 18652* (F); ibid., Borland Road, 14 km by road WNW from Borland Lodge, near South Branch of Borland Burn, W of Monowai, 855–870 m, *Engel 18694* (F); ibid., along flat of Spey River, near W arm of Lake Manapouri, on Doubtful Sound track, 190–230 m, *Schuster 52647*–c. ♂ (F); ibid., Lake Manapouri, Treeman River, *Simpson 36672* (F); ibid., outlet of Lake Te Anau, *Taylor s.n.* as *L. leucophylla* (AK); ibid., off track along East Branch of Eglinton River, SE of Mt. Eglinton and NNE of Te Anau, 440 m, *Engel 18747* (F); ibid., Stuart Mtns., W shore of Lake Thompson N of stream draining from L. Wade, *Fife 7818* as *C. multispinus* (F); ibid., Cascade Creek, near Lake Gunn, tributary of Eglinton River, ca. 305 m, *Child H 3032* as *L. leucophylla* (F); ibid., ibid., near Lake Gunn, Eglinton Valley, *Schuster 55502*–c. ♂ + per. (F); ibid., Central Earl Mtns., Mistake Creek, between Triangle Peak and Melita Peak, NE of N end of Lake Te Anau, 740–800 m, *Engel 18800*–c. ♂ (F); ibid., Lake Marian Track, on Hollyford River, at foot of Mt. Christina, *Schuster 55679* (F); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18853*–c. ♂ (F); ibid., Gertrude Valley, near track entrance to Gertrude Saddle, E of Homer Tunnel, 1740 m, *Engel 21950* (F). **OTAGO:** Catlins River area, Purakanui, NE of Maclennan, ca. 150 m, *Child H 674* as *L. leucophylla* (F); ibid., Ajax Swamp, ca. 1 km N of Ajax Hill, ca. 550 m, *Child H 5543* as *L. leucophylla* (F); Blue Mtns., ca. 455 m, *Child H 5600* as *L. leucophylla* (F); Dunedin, Swampy Hill, ca. 610 m, *Child H 2625* as *L. leucophylla* (F); Leith Valley Bush, near Dunedin, ca. 60 m, *Child H 271* as *L. leucophylla* (F); W slope of Flagstaff, NW of Dunedin, 490–520 m, *Engel 17615*–c. ♂ (F); Mt. Cargill, N of Dunedin, 455–610 m, *Child H 546* as *L. leucophylla* (F); Silverpeaks, N of Dunedin, ca. 455–610 m, *Child H 4737* as *L. leucophylla*, *H 4751* (F); Old Man Range, SW of Alexandra, ca. 1615 m, *Child H 4631* as *L. leucophylla* (F); Kakanui Range, ca. 1220 m, *Child H 2824* as *L. leucophylla* (F); Paradise, Jordan River, head of Lake Wakatipu, ca. 455–520 m, *Child H 453* as *L. leucophylla* (F); Paradise, Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, *Child H 1122* as *L. leucophylla* (F); Route Burn, ca. 520 m, *Child H 2464* (F); Turret Peak, Earnslaw, ca. 455–610 m, *Child H 2469-B* (F); Beans Burn, tributary of Dart River, 455 m, *Child 1283* as *L. leucophylla* (F); Fiordland Natl. Park, above Lake Mackenzie, *Schuster 67-272* (F); ibid., Martin's Bay, N of McKerrow River, *Hatcher 756*, *758* as *L. leucophylla* (F); Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, ca. 1220 m, *Child H 4150* as *L. leucophylla* (F); ibid., ibid., ca. 1370–1470 m, *Engel 17905* (F); ibid., Blue River near confluence with Makarora River, NNE of Makarora, 310 m, *Engel 18916* (F); Siberia Hut, WNW of Makarora, ca. 760 m, *Child H 2913* as *L. leucophylla* (F); opposite Siberia Hut, WNW of Makarora, ca. 1065 m, *Child H 2908* as *L. leucophylla* (F); Cameron Flats, near head of Lake Wanaka, N of Makarora, ca. 305 m, *Child H 174* as *L. aculeata* (F); 0.6–0.7 mi. S of Haast Pass, 505–520 m, *Schuster 55460* (F). **OTAGO/WESTLAND PROV. BOUNDARY:** Mt. Aspiring Natl. Park, summit area of Hasst Pass, 570 m, *Engel 17993*–c. ♂ (F); Mt. Brewster, ca. 1370 m, *Child H 4203* as *L. leucophylla* (F). **WESTLAND:** Mt. Aspiring Natl. Park, below and W of Mt. Armstrong, SSW of Mt. Brewster, 1250–1450 m, *Engel 17798* (F); ibid., off track to Mt. Brewster, below and W of Mt. Armstrong, SW of Mt. Brewster, ca. 900 m, *Engel 17854*–c. sporo. (F); ibid., Mt. Brewster, NE of Haast River, 490–1675 m, *Schuster 67-2716* (F); Haast Pass Road, Cross Creek, just N of Haast Pass, ca. 455 m, *Child H 1899* as *L. leucophylla* (F); Gates of Haast Pass, ca. 455 m, *Child H 510* as *L. leucophylla* (F); Cascade Road, just W of Jackson River, ca. 8–12 km SW of confluence of Jackson and Arawata Rivers, 25–90 m, *Engel 22977*–c. ♂ (F); Jackson Bay, between confluence of Jackson River and Arawata R and Lake Ellery, off Jackson River Road, sea level, *Engel 17924* (F); Fox Glacier, ca. 150 m, *Child H 422* as *L. leucophylla*–c. ♂ (F); near township of Fox Glacier, ca. 0.5–0.6 mi. from front of Fox Glacier, *Schuster 60170*–c. ♂, *60171*–c. sporo. (F); Westland Natl. Park, track to Lake Gault, NE of Lake Matheson, NW of town of Fox Glacier, ca. 100–200 m, *Engel 21709*–c. ♂ (F); Weheka Hills, N of town of Fox Glacier, *Schuster 67-224* as *L. leucophylla* (F); SW slopes of Mt. Hercules, S of Hari Hari, *Schuster 67-2501* (F); Mt. Hercules, *Braggins 75l218* as *L. leucophylla* (AK); Arthur's Pass Natl. Park, N of Hokitika, ca. 90 m, *Child H 3778* as *L. leucophylla*–c. per. (F); Camp Creek, W of Alexander Range, 800–900 m, *ReifC 191*–c. ♂ (F); 5 km N of Runanga, ca. 60–90 m, *Child H 5355* as *L. leucophylla* (F); Paparoa Range, along Croesus Track, ESE of Barrytown, 420 m, *Engel 19328* (F). **WESTLAND/CANTERBURY PROV. BOUNDARY:** Arthur's Pass Natl. Park, Arthur's Pass area, Upper Twin Creek Valley, 930 m, *Engel 18532B* (F); ibid., Arthur's Pass, near Temple Basin Ski Area, *Engel 6468* (F). **CANTERBURY:** Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel 18483* (F); Arthur's Pass vicinity, ¼ mi. W of Bealey Valley, *Whitehouse 29613* (F). **NELSON:** Buller Co., gorge of Fox River, *Fife 4954* as *C. austrigenus* (F); ibid., upper reaches of Waitakere River, on Four Mile Road, ca. 90 m, *Fife 6017* (F); Paparoa Natl. Park, Bullock Creek Road, along Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel 21579*–c. per. (F); Paparoa Range, N side of Tirapahi of Four Mile River, S of Charleston, 145 m, *Engel 19276*–c. ♂ (F); Little Totara River, Madman's Road, ENE of Charleston, ca. 90 m, *Child H 3682* (F); Mt. Arthur Tableland, ca. 1220 m, *Child H 3296* as *L. leucophylla* (F); near Salisbury Lodge, ca. 1065 m, *Brown 88l80b* as *L. leucophylla* (AK); Nelson Lakes Natl. Park, E slope of Robert Ridge in vicinity of Mt. Robert Skifield, W end of Lake Rotoiti, 1400–1480 m, *Engel 22819* (F); ibid., NE margin of Lake Rotoroa, W of St. Arnaud, 520 m, *Engel 21499*–c. ♂ (F). **MARLBOROUGH NEAR BOUNDARY WITH NELSON PROV.:** Kahurangi Natl. Park, Matiri Range, Thousand Acres Plateau, ca. 1100–1200 m, *Engel & von Konrat 27072* (F); Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, ca. 700–920 m, *Engel 21446* (F). **MARLBOROUGH:** Below Pelorus Bridge, *Braggins s.n.* as *L. leucophylla* (AK); Pelorus Bridge, *Braggins s.n.* as *L. leucophylla* (AK); Mt. Stokes, ca. 760 m, *Child H 3246* (F). **NORTH ISLAND. WELLINGTON:** Wellington, *Buchanan s.n.* as *L. leucophylla* (M); ibid., Hawkins Hill, *Moss s.n.* as *L. leucophylla* (AK); Akatarawa, ca. 300 m, *Braggins 84/364F* as *L. leucophylla* (AK); ibid., Waiotauro Road, ca. 670 m, *Braggins 84/376A* as *L. leucophylla*, *84/395A* as *L. leucophylla*, *84/397B* as *L. leucophylla* (AK); Akatarawa Valley, behind Cloustonville, *Braggins s.n.* (AK); Tauherenikau Valley, *Braggins s.n.* (AK); Tararua Range, Akatarawa Forest Park, *Mues NZ 45a* as *L. leucophylla* (F); ibid., Puffer to Smiths Creek track, *Moss s.n.* as *L. villosa* (AK); road between Upper Hutt and Waikanae, near the plateau, *Mues NZ 45* as *L. leucophylla* (F); Hemimatenga Scenic Reserve near Waikanae, *Mues NZ 50* (F); NW Ruahine Range, vicinity between Makirikiri Tarns and Ruahine Corner Hut, ca. 1190 m, *Engel & von Konrat 28095* (F); W Ruahine Mtns., 1–1.5 mi. W of Mt. Mangahuia, ca. 1370 m, *Schuster 67-593* (F); Tongariro Natl. Park, Mt. Ruapehu, Whakapapanui River, *Braggins s.n.* (AK); ibid., Soda Springs, Mangatepopo Stream, NE of Whakapapa Village, 1350 m, *Engel 22492* (F); Mangatepopo Valley, base of Silica Springs, *Braggins s.n.* (AK). **GISBORNE:** Lake Waikaremoana, *Hatcher 1296B* (F); ibid., *Hodgson s.n.* as *L. leucophylla* (AK); ibid., above Aniwaniwa Falls, *Whitehouse 29296*–c. sporo. (F); Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20523* (F); ibid., Lake Waikareiti, *Thompson s.n.* as *L. leucophylla* (AK). **TARANAKI:** Patea, near Whenuakura, *A. Hodgson s.n.* as *L. leucophylla* (F); Pukeiti Bush, near New Plymouth, *Hatcher 416* (F); S side of Mt. Messenger, *Braggins s.n.* as *L. leucophylla* (AK). **SOUTH AUCKLAND:** Whirinaki Forest Park, Waterfall Loop track, near Whirinaki River, *Engel 20699*–c. ♂ + sporo. (F); Mt. Te Aroha, ca. 3 km E of Te Aroha, ca. 480–650 m, *Engel 22154*–c. ♂ (F); Coromandel State Forest Park, Kauraeranga River, 150 m, *Engel 22315* (F); W side of Coromandel Peninsula, in Kauri Clump Forest Reserve, ca. 185–245 m, *Schuster 67-3670* (F); Hunua Falls, *Taylor s.n.* (AK); Mahakinau Road, from Whitianga to Coromandel, *Braggins s.n.* as *L. leucophylla* (AK); Coromandel Peninsula, 6–7 mi. from Whitianga, E side of divide, 75–135 m, *Schuster 67-1530*–c. ♂ (F). **NORTH AUCKLAND:** Howick, Beachlands, *Taylor s.n.* as *L. leucophylla* (AK); Te Whau, *Kirk 533* as *L. leucophylla* (CHR, M); roadside bank, N of Kaiwaka, S of Braigh, *Schuster 67-835* (F); Waipoua Kauri Forest, Wairau Summit, SE of Waimamaku, 390–410 m, *Schuster 67-1818* (F); Waipoua River, ca. 70 m upstream from State Highway 12 bridge, ca. 95 m, *Engel 21060* (F); Puketi Forest, Mokao Ridge, *Braggins s.n.* (AK); opposite Mangamuka Forest Lookout, on State Highway 1, Maungataniwha Range, ESE of Kaitaia, 300 m, *Engel 20970* (F).

***Chiloscyphus mittenianus* var. *obtusus* J. J. Engel**

Chiloscyphus mittenianus var. *obtusus* J. J. Engel, Phytologia 83: 44. 1998 (1997). Holotype: New Zealand, South Is., Otago Prov., Mt. Maungatua, W of Mosgiel, 760 m, *Engel 17768* (F); isotype: (CHR).

Leaves frequently connate dorsally, but rarely uniformly so throughout a given shoot; apex narrowly to occasionally broadly rounded, undivided, entire, the apex rarely and sporadically acute or apiculate; dorsal margin entire; ventral margin mostly 1–3(4) spinose-dentate to laciniate on dilated sector, the distal sector entire, the ventral margin occasionally entire throughout. Underleaves occasionally free on 1 side, but for the most part distinctly connate on both sides.

Differentiation—Variety *obtusus*, which is known from a limited suite of populations, is quite different from well-developed phases of the typical variety, and initially I considered it to be a distinct species. However, after study of the sparsely armed variant of the species (discussed above) and recognition of the full pattern of variation exhibited by the species, it became evident that the sparsely armed variant (Fig. 69: 2) serves as a connecting link between the well-developed, regularly armed phase (Fig. 69: 1, 5, 8–10) and an extreme element, here recognized as a variety. It also became apparent that the rightful position of the extreme element, consisting of the *Engel 17768* population is within the boundaries of *C. mittenianus*, but it nevertheless represents a discrete element separable from the remainder of the species by a suite of several features. First, leaves are often dorsally connate (Fig. 71: 1); I have carefully studied materials of the sparsely armed variant (*Engel 18602*, *18694*) and found leaves uniformly free dorsally. Second, leaf apices are nearly always rounded (see various leaves in Fig. 71). Third, underleaves may be narrowly connate or free on one side in var. *obtusus* (Fig. 71: 9), while they are rather broadly connate on both sides in var. *mittenianus* (Fig. 69: 8) and particularly broadly so in the sparsely armed variant (Fig. 69: 2).

Engel 23258, from 1370–1570 m in the Old Man Range (Otago Prov.), is an interesting population of the var. *obtusus*. Underleaf apices at times are broadly rounded and with only a few teeth; occasional underleaves are completely devoid of teeth except for 1 or 2 teeth in the median portion of the summit. Shoots with such underleaves have a striking resemblance to *C. austrigenus*. The presence of verrucae will immediately distinguish such populations from *C. austrigenus*; presence of verrucae should be checked under the compound microscope.

Distribution and Ecology—The var. *obtusus* is rather rare, and is known from Campbell and Auckland Islands, and in Southland and Otago Provinces, South Is., New Zealand.

The type (South Is.) occurred at 760 m mixed with moss at the edge of a fast-moving stream in a valley with adjacent wet, vertical, rocky cliffs mostly covered by *Blechnum*. In the Old Man Range (Otago Prov.) it occurs at 1370–1570 m in an area of small boggy patches fed by small flushes within alpine vegetation; at this site the variety grows at the lips of rills as well as in flush areas. On South Is. the variety otherwise occurs at 610–1370 m in damp niches under snow tussocks. On Campbell and Auckland Islands the variety occurs in tussock vegetation or in very wet hollows in areas with scrubby vegetation.

Specimens Seen—**CAMPBELL IS.:** *1959/60 Expedition s.n.* as *L. leucophylla* (CHR); Buchanan Valley, 150 m, *Meurk H8284*, *H8285* (WELT); St. Col Ridge, ca. 120 m, *Meurk s.n.* as *L. leucophylla* (CHR); saddle above Lookout Bay, *1960 Expedition s.n.* as *L. leucophylla* (CHR). **AUCKLAND IS.:** Hooker Hills, *Easton H 138* as *L. leucophylla* (CHR); Enderby Is., *Macmillan 83/106* (F); above head of Laurie Harbour, Port Ross, 150 m, *Johnson 14/21* (WELT). **NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, Mt. Burns, Burns Creek headwaters, ca. 1370 m, *Child H 5144* (F); ibid., Expectation Stream, *Zotov s.n.* as *L. leucophylla* (CHR). **OTAGO:** Old Man Range, Symes Road, 1370–1570 m, *Engel 23258*–c. ♂ (F); Lammermoor Range, ca. 610 m, *Child H 3845*, *H 3852*, both as *L. leucophylla* (F).

***Chiloscyphus mittenianus* var. *symmetricus* J. J. Engel**

Chiloscyphus mittenianus var. *symmetricus* J. J. Engel, Phytologia 83: 44. 1998 (1997). Holotype: New Zealand, South Is., Westland Prov., Westland Natl. Park, track to Alex Knob, off track to Louisa Peak, 1170 m, *Engel 18973* (F); isotype: (CHR).

Shoots to 3.2–4.2 mm wide. Leaves uniformly free dorsally; apices subsymmetrically to symmetrically bifid by piliferous lobes, the ventral lobe at most moderately larger than the dorsal, which is only sporadically slightly basal in juxtaposi-

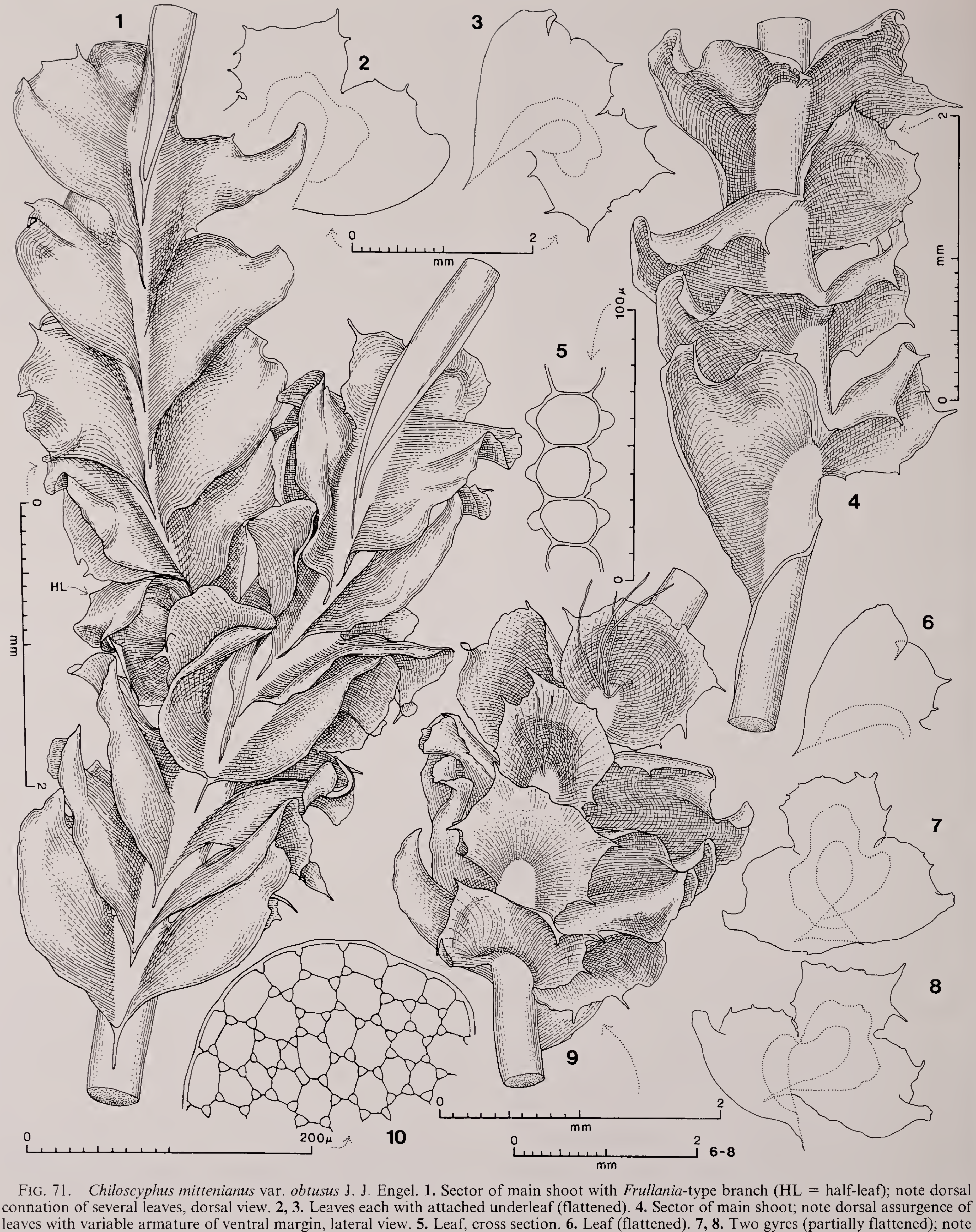

FIG. 71. *Chiloscyphus mittenianus* var. *obtusus* J. J. Engel. **1.** Sector of main shoot with *Frullania*-type branch (HL = half-leaf); note dorsal connation of several leaves, dorsal view. **2, 3.** Leaves each with attached underleaf (flattened). **4.** Sector of main shoot; note dorsal assurgence of leaves with variable armature of ventral margin, lateral view. **5.** Leaf, cross section. **6.** Leaf (flattened). **7, 8.** Two gyres (partially flattened); note differences in armature and extent of connation. **9.** Sector of main shoot, ventral view. **10.** Sector of leaf apex. (Dot-dash line in **2, 3, 6–8** defines basal zone of inflated cells.) (All from holotype.)

tion to the ventral lobe, the ventral lobe terminating in a uniseriate row of 5–7(8) moderately to distinctly elongate cells. Underleaves uniformly broadly connate on both sides.

DIFFERENTIATION—This variant initially may be confused with two other species in the section. The subequal size of the piliferous lobes brings to mind *C. aculeatus*. Variety *symmetricus*, however, is easily separable from that species by the much larger size and the undivided underleaves with apices copiously armed. *Chiloscyphus mittenianus* approaches *C. leucophyllus* via var. *symmetricus*, the two taxa sharing, for example, symmetry of leaf apex and similar number of cells in the uniseriate sector of the ventral lobe. Variety *symmetricus* differs from *C. leucophyllus* by the characters in the key to sect. *Leucophylli* (p. 155; other than those of the leaf apex), and by the much larger stature.

DISTRIBUTION AND ECOLOGY—Known only from a few sites in Southland and Westland Provinces, South Is., New Zealand. The type occurred on the floor of a drainage channel at 1170 m on a south-facing slope in the subalpine zone; here the vegetation was dominated mostly by *Chionochloa*, but with scattered *Dracophyllum* and *Phormium* also present.

SPECIMENS SEEN—**NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, Dusky Sound, Supper Cove, *M. Simpson 3762* as *L. leucophylla* (CHR); ibid., head of Lake Manapouri, *G. Simpson s.n.* as *L. leucophylla* (3 coll.) (CHR).

Subg. *Microlophocolea* (Spruce) J. J. Engel

Lophocolea sect. *Microlophocolea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 426. 1885. *Lophocolea* sect. *Microlophocolea* (Spruce) Schiffn. *in* Engler & Prantl, Natürl. Pflanzenfam. 1 (3): 92. 1893. *Chiloscyphus* sect. *Microlophocolea* (Spruce) Engel & R. M. Schust., Nova Hedwigia 39: 410. 1985 (1984). *Chiloscyphus* subg. *Microlophocolea* (Spruce) J. J. Engel, Novon 9: 22. 1999. Lectotype (*fide* Grolle, 1976): *Lophocolea liebmanniana* Gottsche.

Plants with stems smooth dorsally; leaves with dorsal surface and in some species also the ventral surface hispid; leaf-free gutter lacking, the lines of insertion extending to stem midline dorsally. Plants dioecious or autoecious. Gynoecia either on main shoots or lateral-intercalary branches or, if on ventral-intercalary branches, then with at least a few cycles of vegetative leaves. Capsule wall (where known) with outer face lacking ridges.

Subgenus *Microlophocolea* has four species, three confined to Australasia, and the fourth, *C. muricatus*, is pan-tropical to pan-south temperate. For convenience, all of the species with a hispid leaf surface are included in a single key, as follows.

Key to Taxa with Hispid Leaves

1. Leaf-free gutter broad, 6–10 stem cells wide; stems hispid dorsally; gynoecia usually on abbreviated ventral-intercalary branches lacking vegetative leaves; outer face of capsule wall with a network of hyaline ridges. Plants dioecious; leaves of well-developed plants undivided; oil-bodies bluish or hyaline. New Zealand, Tasmania, Australia (Vict.) . . [*Cyanolophocolea echinella*] (p. 203)

1. Leaf-free gutter lacking, the lines of insertion extending to stem midline dorsally; stems smooth dorsally; gynoecia either on main shoots or lateral-intercalary branches or, if on ventral-intercalary branches, then with at least a few cycles of vegetative leaves; outer face of capsule wall (where known) without ridges. Subg. *Microlophocolea* 2

  2. Underleaf lobes with opposing teeth or cilia, the abaxial surface of both lobes and lamina often with scattered echinae; ventral surface of leaf (suboptimal plants aside, cf. p. 191) with echinae; ventral-intercalary branches at least sometimes present. Sect. *Microlophocolea* 3

    3. Plants small, to 1 mm wide; echinae of dorsal surface of leaf juxtaposed over the lumen of lamina cells; stems lacking paraphyllia ventrally; lateral-intercalary branches absent; median leaf cells 14–18 × 17–20 µm; stems, in section, 6–7 cells high; leaves consistently bifid; underleaves 2-lobed; plants autoecious. New Zealand, Tasmania, Australia (Vict.) (Pantropical) . . . . *C. muricatus* (p. 196)

    3. Plants medium, to 2.2 mm wide; teeth of dorsal surface of leaf juxtaposed either over the radial walls or the lumen of lamina cells; stems paraphyllose ventrally; lateral-intercalary branches common; median leaf cells 22–29 × 25–31 µm; stems, in section, 12–13 cells high; leaves shallowly bifid or (often) undivided; underleaves 2–4-lobed; plants dioecious. New Zealand . . . . *C. villosus* (p. 190)

  2. Underleaf lobes entire or at most with 1–2 teeth, the armature never regularly opposing, the abaxial surface of both lobes and lamina smooth; ventral surface of leaf smooth, lacking all traces of armature; ventral-intercalary branches lacking. Plants dioecious. Sect. *Hemispini* 4

    4. Surface echinae 1(2) celled, juxtaposed over the lumen of most lamina cells; shoots with leaves uniformly hispid, consistently bifid, not with apices polymorphic; perianth and both surfaces of gynoecial bracts hispid. New Zealand . . . . *C. parvispineus* (p. 182)

    4. Surface echinae 1–3 celled, never predominantly unicellular, juxtaposed over the radial walls or the lumen of cells all or mostly in dorsal half of leaf; shoots often with some leaves smooth, with apices often polymorphic: undivided and entire to spinose dentate to short bifid, often on 1 shoot; perianth and gynoecial bract surfaces smooth. Tasmania, Australia (Vict., A.C.T., NSW) . . . . *C. gippslandicus* (p. 187)

Sect. *Hemispini* J. J. Engel

Chiloscyphus sect. *Hemispini* J. J. Engel, Novon 9: 23. 1999. Type: *Chiloscyphus parvispineus* J. J. Engel.

Branches common, mostly of lateral-intercalary type, less often of *Frullania* type; ventral-intercalary branches lacking; leaves with dorsal surface hispid, the ventral surface of leaf uniformly smooth; underleaf lobes entire or at most with 1–2 teeth, the teeth never regularly opposing, the abaxial surface of both lobes and lamina smooth. Plants dioecious.

This strictly Australasian section contains two species, *C. parvispineus* of New Zealand and *C. gippslandicus* of Australia (for key see above, this page).

Chiloscyphus parvispineus J. J. Engel

Chiloscyphus parvispineus J. J. Engel, Phytologia 83: 44. 1998 (1997) ("*parvispinus*"). Holotype: New Zealand, Otago Prov., S side of Mt. Cargill, just below summit, N of Dunedin, ca. 2200 m, *Engel 17563* (F); isotype: (CHR).

Plants with the general appearance of *Geocalyx*, soft, loosely prostrate to rather closely adnate, pale to whitish green to olive green; shoots medium, to 2.2 mm wide. Branches common, of lateral-intercalary type and often not to barely extending beyond leaf apices of parent axis, the branches sporadically of *Frullania* type (the half-leaf undivided or asymmetrically short bifid). Stems smooth, without surface processes, 9–10 cells high, the cortex undifferentiated ventrally but on dorsal side of stem consisting of slightly larger cells, with both cortex and medullary cells thin walled. Rhizoids from stem in a rather narrow zone at immediate base of underleaves, the tips often highly ramified. Leaves ± inflated in appearance, subopposite, subhorizontal, strongly dorsally assurgent in basal portion, widely spreading, rather densely imbricate, free dorsally, with orientation strongly succubous, the insertion not to very slightly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement very regular and covering much of stem in dorsal view except for narrow V-shaped sectors between opposing leaves. Leaves with dorsal surface, except near the ventral base, densely echinate, armed with 1(2)-celled short, conical projections which are juxtaposed 1 each over the lumen of most cells, the ventral surface completely smooth; leaves strongly broadly convex, the apices sometimes oriented at ca. 90° with remainder of leaf, the leaves asymmetrically deltoid to ovate, clearly widest near base; apex bifid to 0.15–0.2, with lobes ± parallel, plane, unequal, the ventral distinctly larger and longer, the lobes medium acute, terminating in a uniseriate row of (1)2(–4) cells, lobe margins with opposing 1(–2) celled sharp teeth; dorsal margin straight to faintly rounded, plane to moderately but sharply deflexed, regularly and copiously denticulate to the base by 1 (exceptionally 2)-celled sharp, conical teeth which are of similar size throughout, the base not decurrent; ventral margin broadly and slightly rounded, plane, irregularly spinose-dentate to small-laciniate. Leaf cells with walls thin, trigones large and bulging to knot-like, median leaf cells with and without spines of similar size, 18–24 μm wide and long. Oil-bodies in all lamina cells (with or without spines), but absent from surface echinae (which have chloroplasts and oil-droplets), occupying ca. 50–70% of cell lumen, faintly light grey, 3–5 or 5–9 per cell, moderately to coarsely papillose, with age becoming increasingly strongly papillose, ovoid to narrowly to broadly elliptic, occasionally subcrescentic, 9.8–11.1 × 3.9–4.6 μm. Underleaves much smaller than leaves, 1.5–2× stem width, narrowly connate on both sides, the insertion symmetric, inverted shallowly U-shaped, the underleaves strongly spreading, distant to approximate, with both surfaces smooth, the lamina plane to slightly concave (ventral view); underleaves cuneate, bifid to 0.65–0.75; lobes diverging, subcaudate to caudate, terminating in a uniseriate row of several cells, the lobe margins entire or with 1 or 2 teeth, rarely with several teeth and a prominent lacinium on 1 or both margins, the lobe ornamentation rarely opposing; lamina margins often slightly recurved, 1–3-dentate-laciniate. Asexual reproduction absent.

Plants dioecious. Androecia subspicate to subfolious, even on 1 shoot, on main shoot or short (and sometimes without vegetative leaves) to elongate lateral-intercalary branches, or (less often) on rather long *Frullania*-type branches, the androecia terminal but eventually becoming intercalary; bracts variable, of 2 intergrading types: 1) somewhat smaller than to subequal to leaves in size, the bracts of similar form as vegetative leaves except for the development of a dorsal pocket; and 2) much smaller than leaves, and either mostly ventricose except for the abruptly reflexed apex or the entire bract strongly ventricose-cucullate, so much so that the dorsal pocket is ill-defined and the apex is plane; bracts of both types erect to strongly spreading, strongly dorsally assurgent, loosely appressed to bract immediately above, the abaxial and adaxial surface of saccate portion smooth, the saccate portion fused toward base with opposite bract; bracts of both types with the distal portion gently to abruptly deflexed, bifid and with dorsal surface ornamented as in vegetative leaves, the ventral margin armed as in vegetative leaves. Lobule large to rather small for bract size, the margin inflexed, crenulate and with copious huge pyriform slime papillae; antheridia solitary, large for bract size, the stalk uniseriate. Gynoecia on main shoot or short to long lateral-intercalary branches, the length of the intercalary branches variable: at times without vegetative leaves, at times with only a few cycles of vegetative leaves, sometimes considerably longer; subfloral innovations lacking; vestigial stem perigynium present, with 1–2 cycles of bracts and bracteoles inserted on the vestigial perigynium. Bracts of innermost series much larger than leaves, transversely oriented, the basal portion ensheathing perianth, the distal half abruptly and sharply deflexed and ventrally secund, the bracts free from one another, the basal (ensheathing) portion plane or more often with a broad concavity, the distal portion broadly convex, the bracts asymmetrically elliptic, the dorsal margin more strongly arched than the ventral, the dorsal surface armed with 1–2-celled echinae in distal half and in a strip along dorsal margin nearly to bract base, the ventral half otherwise smooth, the ventral surface armed with scattered sharp echinae in median third and sparingly so in distal third; apices ± symmetrically short bifid by medium acute lobes with margins armed with opposing, short, 1–2-celled teeth; dorsal margin of lamina sharply and abruptly reflexed to revolute and forming a cnemis, the margin copiously spinose dentate nearly to the base; ventral margin of lamina plane or less often sharply inflexed, spinose dentate, but more sparingly and irregularly so than the dorsal margin. Bracteoles of innermost series much smaller than bracts, ca. 0.4× bract area, free or narrowly connate on 1 side, the basal half broadly convex (ventral view), the distal half of adaxial surface armed with 1–2-celled echinae, the basal half and abaxial surface smooth; bracteoles elliptic to rhomboid, with apices bifid to 0.3–0.5 by ventrally sulcate, narrowly acuminate lobes with margins armed as in bract lobes; lamina margins with a small to large lacinium at ± the level of the sinus base, the margin otherwise sparingly and sharply denticulate distally and subentire below. Perianth longly exserted beyond bracts, often slightly to decidedly inflated, trigonous but not sharply so, elliptic to narrowly ovate to ovate-oblong, the surface, except for the basal ca. 0.2, densely hispid with echinae similar to those of dorsal surface of leaf; perianth narrowing to ± straight toward the ± wide, shallowly 3-lobed mouth; lobes shallowly bifid, the segments acuminate, with margins spinose dentate, the teeth opposing,

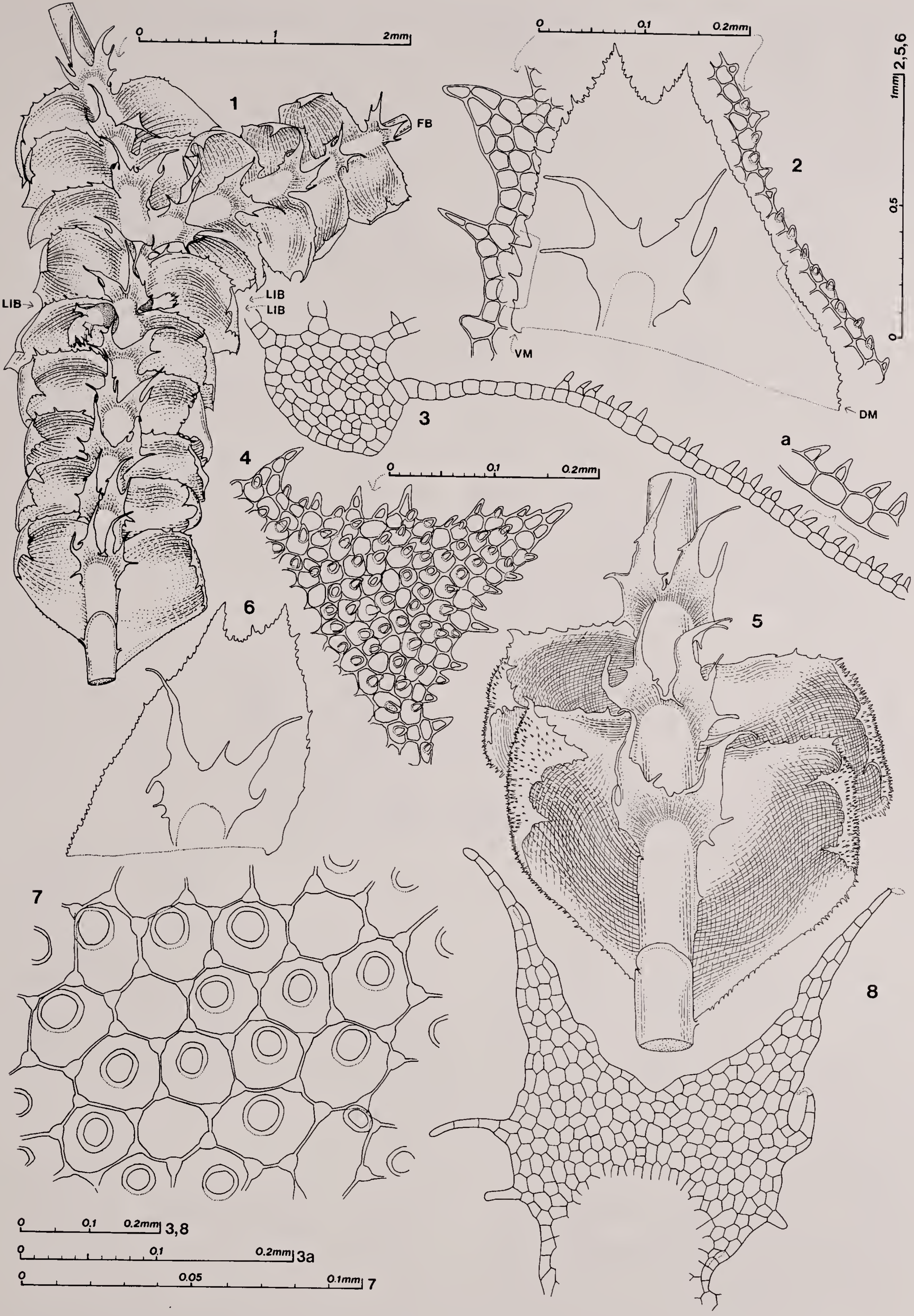

FIG. 72. *Chiloscyphus parvispineus* J. J. Engel. **1.** Shoot with two lateral-intercalary branches (= LIB) and a *Frullania*-type branch (= FB), ventral view (leaf surface teeth not shown). **2.** Leaf and within, underleaf; dotted lines at margin of leaf on either side indicate portions drawn at higher magnification. **3.** Cross section through stem and median portion of leaf and detail of bracketed portion of leaf (= a). **4.** Ventral segment of leaf. **5.** Portion of axis, ventral view. **6.** Leaf and within, underleaf. **7.** Median leaf cells, the rings indicate spine bases. **8.** Underleaf. (All from holotype.)

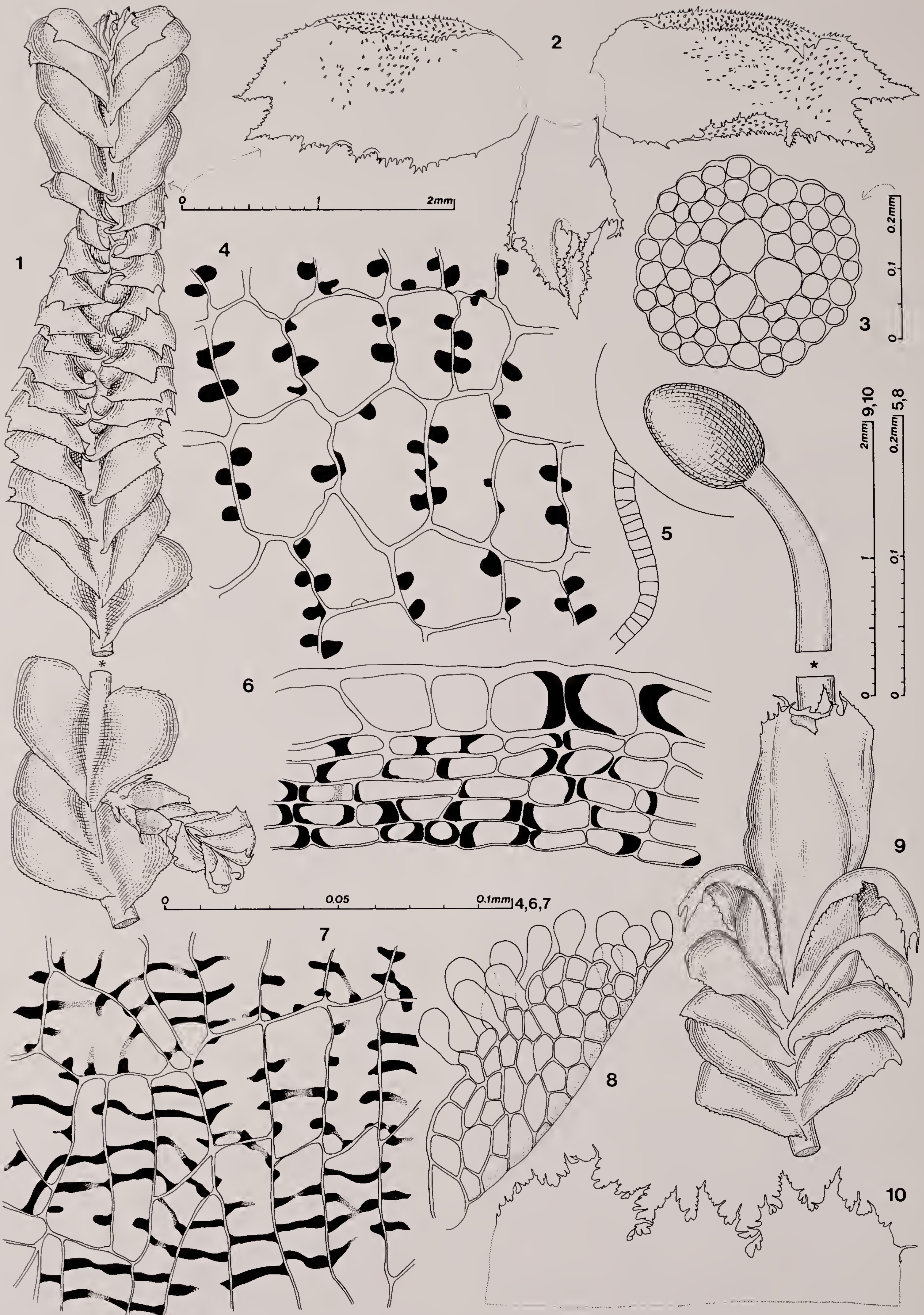

FIG. 73. *Chiloscyphus parvispineus* J. J. Engel. **1.** Androecia intercalary on main axis and on abbreviated lateral-intercalary branch (leaf surface teeth not shown). **2.** ♀ Bracts and, lower, bracteole showing abaxial (ventral) surface. **3.** Seta, cross section. **4.** Capsule wall, outer layer. **5.** Antheridium. **6.** Capsule wall, cross section. **7.** Capsule wall, inner layer. **8.** ♂ Bract, free margin of lobule. **9.** Gynoecium, with mature sporophyte (leaf surface teeth not shown). **10.** Perianth mouth, ventral lobe in middle (surface teeth not shown). (All from holotype.)

mostly 1–2-celled but a few larger, the lobes otherwise laciniate-lobulate and spinose dentate. Calyptra small, extending ca. half the perianth length at maturity.

Seta 8–9 cells in diam., with 23–25 rows of outer cells surrounding an inner core of scattered cells of similar size or slightly larger, the inner core, however, with 3–5 much larger cells which average 1.6× the diameter of other core cells, the inner core cells with corners thickened as in medium to large sized trigones. Capsule ellipsoid to ellipsoid-subovoid, 840–980 µm × 595–700 µm, the wall 52–56 µm thick, of 6–7 (occasionally locally 5) layers, the outer layer of cells equal to thickness of 2.2–2.9 of interior strata; outer layer of cells subquadrate to short rectangular, the radial walls moderately but irregularly thickened, with red-brown nodular thickenings, the thickenings mostly on longitudinal walls and only sporadically on transverse walls, the exposed tangential wall rather thickened, in surface and cross section appearing smooth; intermediate layers each thicker than inner layer, the intermediate layers with vertical thickenings often considerably tangentially extended, sometimes becoming semiannular; innermost layer of cells irregularly short to long and narrowly rectangular, the walls thin, with semiannular bands red brown, common, rather widely spaced, sporadically nonpigmented in median portion, sometimes incomplete, rarely forked, the radial walls with nodular and spine-like thickenings sometimes present on both longitudinal and transverse walls.

Spores 13.5–14.4 µm, light brown, with faint, dense, low, close, papillose and short-vermiculate markings; spore:elater diameter ratio 1.6–1.9:1. Elaters moderately tortuous, 7.7–8.6 µm wide, the spirals 2.4–3.4 µm wide.

VARIATION—A variant of this species may be confusing. The leaves are so strongly reflexed that they make contact with the underleaves or partially overlap them (Fig. 74: 2). This lends the plants a terete appearance, particularly in ventral view. Due to this unusual leaf orientation, there is no indication of the bifid-leaved condition in dorsal view (Fig. 74: 1); thus, such specimens at first glance may be confused with *C. villosus*. Furthermore, such plants also tend to have underleaves with a prominent lacinia-lobule near the base of 1 or both of the lateral margins of the lobes (Fig. 74: 1), thereby giving the superficial appearance of being weakly 4-lobed, a characteristic of *C. villosus*. (Such prominent ornamentation occurs more often on the lateral margin of the lobe, and rarely on both the margin defining the sinus and the lateral margin.) This variant further deviates from typical plants in having narrower leaves with margins more weakly armed (Fig. 74: 3). Characters in the key, however, will immediately identify this variant as *C. parvispineus*. An example of this variant is *Engel 18547*; a somewhat intermediate condition occurs in *Engel 18988*, where only certain shoots are terete.

Particular care should be taken with small forms of this species because of the resemblance of such plants to those of *C. muricatus*. Characters found in the key will distinguish the plants.

DISTRIBUTION AND ECOLOGY—This New Zealand endemic ([305–]510–1740 m) is rather common in wet forests, especially of *Nothofagus*. It occurs, for example, in middle to upper elevation *Nothofagus menziesii* forests, as well as in forests of *Nothofagus menziesii–N. fusca* or *N. solandri–N. fusca* or *N. solandri*. In woodlands it occurs on bryophyte covered logs, tree trunks of various sizes (at times occurring only in small patches), on rotted stumps and on boulders or rocky outcrops, particularly in niches where soil has accumulated. It only sporadically occurs on earth. The species is able to tolerate some exposure. For example, at Roberts Point Track in the Franz Josef Glacier Valley (ca. 510–570 m) it occurs in areas of mostly exposed, bare rock with only a few scattered shrubs and grasses (*Engel 18133*), and at this site it occurs over wood. The species also occurs in ecotonal areas between *N. menziesii* forest and the alpine tussock zone. In the subalpine zone the species occurs on exposed, well-drained slopes in areas dominated mostly by *Chionochloa* (1170 m, track to Alex Knob, Westland Natl. Park, *Engel 18988*), as well as on boulder faces (especially where some soil has accumulated) in mosaics of large boulders and dense subalpine scrub (1740 m, Gertrude Valley, Fiordland Natl. Park, *Engel 21952*).

On North Is. it is found in a variety of forest types in addition to those of *Nothofagus*. For example, it occurs in mossy *Dacrydium biforme–Olearia* forests, kamahi–podocarp forests as well as wet, mature *Dacrydium–Metrosideros–Weinmannia* woodlands. At upper elevations on North Is. it occurs on branches of *Olearia* in mosaics of stunted *Olearia colensoi* (leatherwood) and tussock (1265–1320 m, the summit area of Te Rangaakapua, Urewera Natl. Park, *Engel 23444*).

SPECIMENS SEEN (selected)—**NEW ZEALAND. SOUTH ISLAND. SOUTHLAND:** Fiordland Natl. Park, off track to Island Lake, just W of Borland Saddle, S of S Branch of Borland Burn, W of Monowai, 800 m, *Engel 18632*–c. ♂ (F); ibid., summit of Borland Saddle, off track to Mt. Burns, S of S Branch of Borland Burn, W of Monowai, 1090 m, *Engel 18660*–c. sporo. (F); ibid., Borland Road, 14 km by road WNW from Borland Lodge, near S Branch of Borland Burn, W. of Monowai, 855–870 m, *Engel 18699*–c. ♂ (F); ibid., Cascade Creek, near Lake Gunn, tributary to Eglinton River, ca. 305 m, *Child H 2626* as *L. muricata*–c. per. (F); ibid., near road between Homer Tunnel and Te Anau, *Hatcher 1551*–c. per. (F); ibid., Gertrude Valley, near track entrance to Gertrude Saddle, E of Homer Tunnel, 1740 m, *Engel 21952* (F); ibid., Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel 23209* (F). **OTAGO:** Maungatua, W of Mosgiel, ca. 915 m, *Child H 4100* (F); above Leith Stream Valley, on saddle to Waitati, Dunedin, *Allison H 910* as *L. villosa* (CHR); Flagstaff, NW of Dunedin, ca. 610 m, *Child H 1664* as *L. muricata* (F); Mt. Cargill, cliffs on S side, just below summit, N of Dunedin, ca. 670 m, *Engel 17563*–c. sporo. + ♂ (F); ibid., N of Dunedin, 610–700 m, *Child H 2670* as *L. muricata*–c. ♂, *H 2671* as *L. villosa*–c. per. (F); ibid., bush on NE face, N of Dunedin, ca. 550 m, *Allison H 5312* as *L. muricata* (CHR); Fiordland Natl. Park, Humboldt Mtns., between Lake Howden and the Eglinton–Hollyford Divide, *Schuster 67-3580a* (F); ibid., ibid., above Lake Mackenzie, *Schuster 67-286* (F); ibid., ibid., N of Earland Falls, on track to Lake Mackenzie, *Schuster 67-3457* (F); ibid., trail between Gunn's Hut and Hidden Falls, ca. 30 mi. SE of Lake McKerrow, *Hatcher 582*–c. ♂ (F); Mt. Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makaroa River, 430–480 m, *Engel 21914*–c. per. (F). **OTAGO/WESTLAND PROV. BOUNDARY:** Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel 17980*–c. sporo. (F). **WESTLAND:** Mt. Aspiring Natl. Park, off track to Mt. Brewster, below and W of Mt. Armstrong, SW of Mt. Brewster, ca. 900 m, *Engel 17852*–c. sporo. + ♂ (F); Westland Natl. Park, Franz Josef Glacier Valley, off Roberts Point Track, SW of Mt. Gunn, ca. 510–570 m, *Engel 18133* (F); ibid., track to Alex Knob, off track to Louisa Peak, 1170 m, *Engel 18988* (F); Camp Creek, W of Alexander Range, 905–1040 m, *Reif C126H*–c. sporo. (F); Paparoa Mtns., N flank of Mt. Euclid, ca. 1100 m, *Beever s.n.* as *L. muricata* (AK); ibid., ibid., ca. 0.5 km SE of Morgan Tarn, 1005–1065 m, *Fife 6456* as *L. muricata* (F). **WESTLAND/CANTERBURY PROV. BOUNDARY:** Arthur's Pass Natl. Park, Arthur's Pass area, overlooking Upper Twin Creek Valley, 1010 m, *Engel 18547* (F); ibid., Bealey Valley Track, ca. 875–900 m, *Engel 22887*–c. sporo. (F). **CANTERBURY:** Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel 18485* (F); ibid., near Bealey Glacier Vista, *Engel 6852* (F). **NELSON/CANTERBURY PROV. BOUNDARY:** Spencer Range, Mt. Gloriana, ca. 1220 m, *Child H 3969* as *L.*

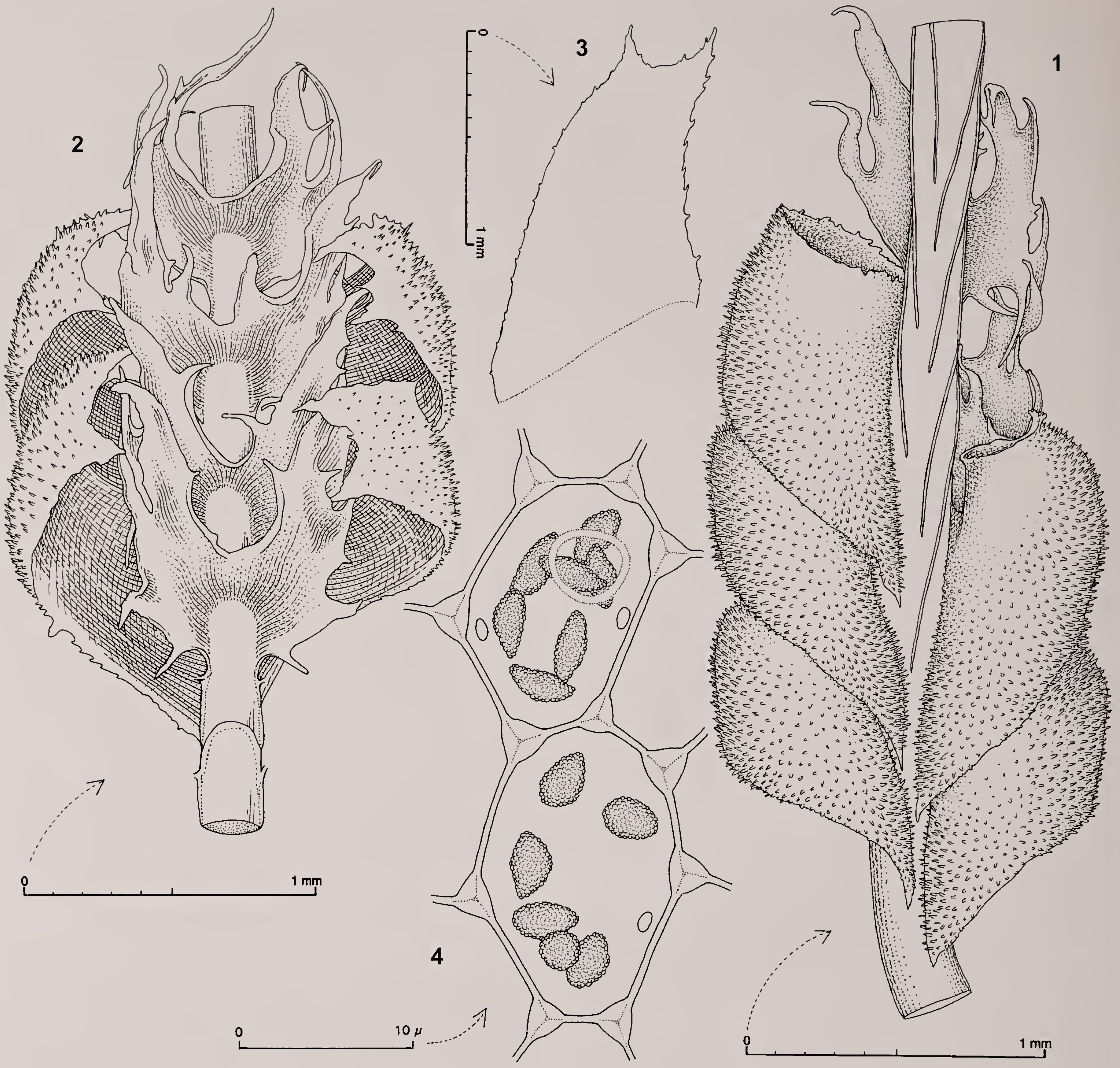

FIG. 74. *Chiloscyphus parvispineus* J. J. Engel. **1.** Portion of main shoot of terete variant, dorsal view. **2.** Portion of main shoot of terete variant, ventral view. **3.** Leaf from terete variant. **4.** Oil-bodies of median leaf cells, the upper cell with spine base indicated. (**1–3,** from *Engel 18547*, New Zealand, South Is., Arthur's Pass Natl. Park; **4,** from *Engel 27964*, New Zealand, North Is., Gisborne EP, Raukumara Forest Park, Raukumara Range, vicinity of peak of Raukumara.)

muricata (F). **NELSON:** Kahurangi Natl. Park, Matiri Range, Thousand Acres Plateau, ca. 1100–1200 m, *Engel & von Konrat 27062* (F); Nelson Lakes Natl. Park, Pinchgut Track, W of southern sector of Lake Rotoiti, ca. 1280–1390 m, *Engel 21417*–c. per. (F); Mt. Arthur, Tableland Track, *Sainsbury s.n.* as *L. muricata* (CHR). **MARLBOROUGH:** Mt. Stokes, *Zotov s.n.* (CHR). **NORTH ISLAND. WELLINGTON:** Akatarawa, *Braggins 84/442* as *L. muricata* (AK); Te Matawai, *Zotov s.n.* as *L. muricata*–c. ♂ (CHR); Schormann's Track near Mt. Hines, 10–12 mi. W of Eketahuna, 885–1005 m, *Schuster 49167B* (F); Tongariro Natl. Park, ca. 7 km from Ohakune on Ohakune Mtn. Road, ca. 900 m, *Engel 21347* (F). **HAWKE'S BAY:** Wairoa, "Kiwi," *Hodgson 443* as *L. variabilis* (CHR); Makaretu Stream, near Wairoa, *Hodgson 409* as *L. variabilis* (CHR). **TARANAKI:** Mt. Egmont Natl. Park, near Stratford Mtn. Road, E slope of Mt. Egmont, ca. 610 m, *Schuster 48940B* (F). **GISBORNE PROV.:** Urewera Natl. Park, Huiarau Range, summit area of Te Rangaakapua, 1230–1320 m, *Engel 23500*–c. per. + ♂ (F); Raukumara Range, Raukumara Forest Park, vicinity of peak of Raukumara, ca. 1350 m, *Engel & von Konrat 27964* (F). **NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY:** Urewera Natl. Park, crest trail from Highway 38 toward Whakataka summit, N of northern extremity of Lake Waikaremoana, 930–1030 m, *Engel 20638*–c. sporo. + ♂ (F). **SOUTH AUCKLAND:** Whirinaki Forest Park, Waterfall Loop track, near Whirinaki River, SSW of Minginui, *Engel 20704*–c. per. (F); Lake Taupo area, SE slopes of Mt. Tihia, 5 mi. W of Turangi, 760–915 m, *Schuster 67-644* (F); Roto-a-kui Bush, E of Taupo, ca. 670 m, *Allison H 3616* as *L. muricata*–c. per. (CHR); Ruahakunui Bush, E of Taupo, ca. 670 m, *Allison H 3615* as *L. muricata*–c. per. (CHR); Herangi Range, Whareorino Forest, tributary of Awakino River, W of Leitchs Road, and SW of Te Kuiti township, 285 m, *Engel & von Konrat 23928* (F). **NORTH AUCKLAND:** Auckland, Withiel Thomas Reserve, *Braggins s.n.* (AK); Waipoua Forest, *Allison H 743* as *L. muricata* (CHR); Waima Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, off Waiotemarama Track, 650–680 m, *Engel 22621*–c. sporo. (F). CHATHAM IS.: Southern Tablelands, Te Mangahou Creek, 40 m, *de Lange CH1987* (AK, F).

Chiloscyphus gippslandicus J. J. Engel & R. M. Schust.

> *Chiloscyphus gippslandicus* J. J. Engel & R. M. Schust., Nova Hedwigia 39: 415. 1985 (1984) *ut nom. nov. pro Lophocolea lauterbachii* Steph., Bull Herb. Boissier 6(11): 938. 1906 (= Spec. Hep. 3: 118), *non Chiloscyphus lauterbachii* Steph., Bull. Herb. Boissier 7(10): 839. 1907 (= Spec. Hep. 3: 211). Lectotype (*nov.*): Australia, [Victoria], Gippsland, Lake Tyers, 15 Nov. 1889, *Lauterbach 230* (G!–c. ♂ + young ♀).

Plants sometimes with complete shoot appearing like *C. semiteres*, but in other populations the shoots are frequently polymorphic: part of shoot (particularly distal sectors) is smooth-leaved and with a striking resemblance to *C. semiteres* in both dorsal and ventral views, while some, particularly lower sectors, appear like *C. rupicola* or luxuriant *C. muricatus* and are hispid-leaved; plants soft, loosely prostrate to closely adnate, light green; shoots small and 1.2–1.8 mm wide to medium and 2–2.2 mm wide. Branches common, mostly of lateral-intercalary type, sometimes submicrophyllous, the branches less often of *Frullania* type; branch leaves often smooth. Stems smooth, without surface processes, 7–8 cells high, the cortex feebly differentiated, the cells subequal in size to medullary cells but distinctly thicker walled, the medullary cell walls thin or slightly thickened. Rhizoids mostly from stem at immediate base of underleaves, but several at times midway between 2 underleaves, the tips often highly ramified. Leaves alternate, subhorizontal, often dorsally assurgent in basal portion, widely spreading, rather densely imbricate, free dorsally, with orientation strongly succubous, the insertion not recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells, the leaf arrangement allowing exposure of considerable stem tissue in dorsal view. Leaves with dorsal surface echinate, armed with 1–3-celled short projections which are juxtaposed either over the radial walls or the lumen of lamina cells, the ornamentation all or mostly on dorsal half of leaf and especially on leaves in median or basal sectors of shoot, the ventral surface completely smooth; leaves broadly convex, at times strongly so, the leaves a- to subsymmetrically ovate to deltoid, widest near base; apex in some populations all or predominantly undivided and entire, in other populations polymorphic and unlobed and entire to sparingly to rather densely spinose dentate, the apex often short bifid and then with lobes ± parallel, plane, subequal or unequal (and with the ventral larger and longer), the lobes apiculate to acuminate to, occasionally medium acute, terminating in a uniseriate row of 2–4 cells, the lobe margins entire or with opposing 1(2)-celled teeth, the intervening sinus often armed; dorsal margin straight to broadly and gently rounded, plane to rather sharply deflexed, entire or irregularly dentate/spinose-dentate nearly to the base, the smaller teeth 1-celled, the larger terminating in a uniseriate row of to 5 cells, the margin somewhat decurrent at base; ventral margin broadly and slightly rounded, plane, irregularly spinose-dentate or entire. Leaf cells with walls thin, trigones variable: in some populations minute to small to medium, in others medium to ± knot-like, median leaf cells with and without spines of similar size, 20–28 µm wide and long; surface smooth. Oil-bodies pale, transparent (*Meagher 1673*). Underleaves with appearance of those of *C. semiteres* var. *semiteres*, much smaller than leaves, 1.8–2.9× stem width, free or narrowly but distinctly connate on 1 side, the insertion sometimes asymmetric, inverted shallowly U-shaped, the underleaves at most slightly spreading, approximate to contiguous, with both surfaces smooth, the lamina plane to slightly convex (ventral view); underleaves subrectangular to ovate, bifid nearly to base, sporadically less deeply divided and then bifid to ca. 0.7, the lobes ± parallel to diverging, acuminate to caudate, terminating in a uniseriate row of several cells, the lobe margins entire or sporadically with 1–2 ciliiform processes toward base of margin defining sinus; lamina margins plane, with a process grading from laciniiform to lobuliform (the underleaves then 4-lobed), the lamina margins often with 1–2 accessory teeth or laciniae. Asexual reproduction by sporadic regeneration from leaf lobes.

Plants dioecious. Androecia on leading shoots or rather short, indeterminate lateral-intercalary branches, variable, of 2 intergrading types, the extremes being 1) subfolious, the bracts of similar basic shape as vegetative leaves but somewhat smaller, the bracts widely spreading, ventricose and dorsally assurgent in basal portion, the distal portion soon becoming subhorizontal and slightly convex, the lobule small in proportion to bract size; and 2) subspicate, the bracts much smaller than leaves, strongly dorsally assurgent and vertical, erect throughout or the distal sector somewhat deflexed, the dorsal pocket large in proportion to bract size; bracts of both types with apex variability as in leaves, the dorsal surface smooth or hispid, the bracts with saccate portion smooth in profile, the saccate portion fused toward base with opposite bract. Lobule margin inflexed, the apex rounded or with a cuspidate process, the free margin crenate-dentate, with a few slime papillae; antheridial solitary, the stalk uniseriate. Gynoecia on main shoot or short to long lateral-intercalary branches, the length of the intercalary branches variable: at times without vegetative leaves, at times with several cycles of vegetative leaves; subfloral innovations lacking; vestigial stem perigynium present, with 2 cycles of bracts and bracteoles inserted on the vestigial perigynium. Bracts of innermost series much larger than leaves, transversely to subsuccubously oriented, at least the basal portion ensheathing perianth, the distal half often abruptly and sharply deflexed, the bracts free from one another, the basal (ensheathing) portion with a broad concavity, the distal portion broadly convex, the bracts asymmetrically elliptic, the dorsal margin more strongly arched than the ventral, the dorsal and ventral surfaces smooth; apices undivided and entire or sparingly dentate to short bifid by rounded or apiculate to acuminate lobes; dorsal margin of lamina plane or reflexed, entire or with a few teeth; ventral margin of lamina plane or inflexed or reflexed, entire or with a tooth. Bracteoles of innermost series much smaller than bracts, broadly connate on 1 side, broadly convex to concave (ventral view), the adaxial and abaxial surfaces smooth; bracteoles subrectangular to subelliptic, with apices bifid to ca. 0.3–0.55 by plane to ventrally sulcate, acuminate to subcaudate lobes with margins entire or with a tooth; lamina margins with a lacinium at ± the level of the sinus base or sometimes situated on the outer lobe margin, the margins otherwise with a dentiform to laciniiform process or entire. Perianth longly exserted beyond bracts, trigonous throughout, obovate, the surface smooth; perianth broadening toward the ± wide, shallowly 3-lobed mouth; lobes shallowly bifid, the

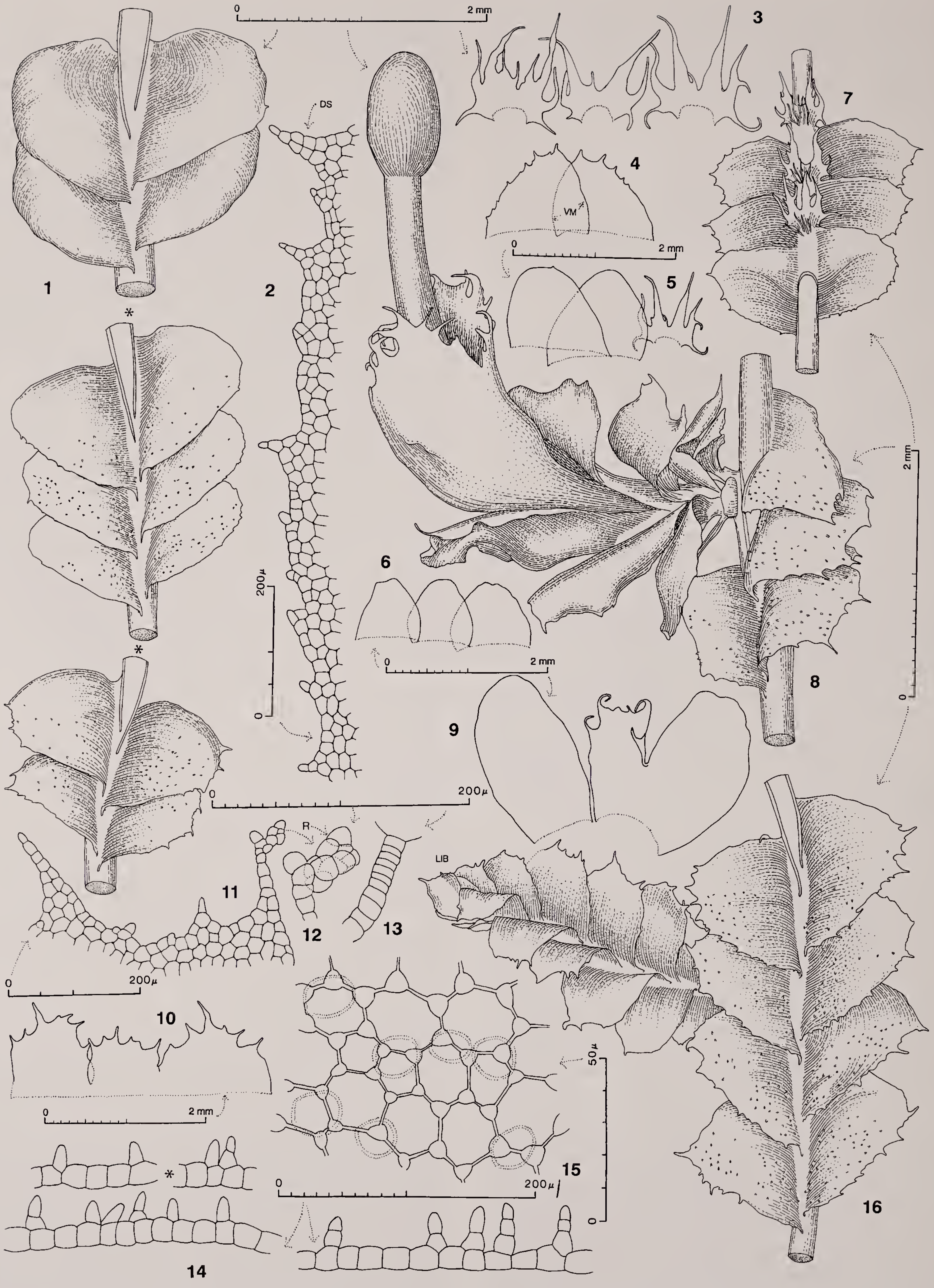

FIG. 75. *Chiloscyphus gippslandicus* J. J. Engel & R. M. Schust. **1.** Distal, median and basal sectors of a single main shoot, dorsal view. Note differences of apex and surface armature. **2.** Sector of dorsal margin showing irregular armature (ds = dorsal segment). **3.** Underleaves from 1 shoot. **4.** Leaves from 1 shoot (vm = ventral margin). **5.** Leaves and an underleaf from 1 shoot. **6.** Leaves from 1 shoot. **7.** Sector of main shoot, ventral view. **8.** Main shoot with hispid leaves and an abbreviated, lateral-intercalary branch with all bract and perianth surfaces smooth (the leaf above branch base removed for clarity), dorsal view. **9.** ♀ Bracts and in middle, bracteole. **10.** Perianth mouth, ventral lobe in middle. **11.** Leaf apex with regenerant (= r) on ventral segment. **12.** Regenerant. **13.** Antheridium. **14.** Leaf cross sections. **15.** Median leaf cells, the stippled rings indicate bases of surface teeth (note knot-like trigones). **16.** Median sector of main shoot with lateral-intercalary branch (= LIB), dorsal view. (1–

segments acuminate, with margins dentate-laciniate or entire, the lobes otherwise dentate-laciniate below level of segments. Calyptra extending ca. 0.7 the perianth length at maturity.

Capsule ellipsoid, 945 µm × 700 µm, the wall 32–34 µm thick, of 5 layers, the outer layer of cells equal to thickness of 2–2.5 of interior strata; outer layer of cells subquadrate to short rectangular, the radial walls with red-brown nodular thickenings, the thickenings mostly on longitudinal walls and only sporadically on transverse walls, the exposed tangential wall rather thickened; intermediate and inner layers subequal in thickness, the intermediate layers with vertical thickenings often considerably tangentially extended; innermost layer of cells irregularly short to long and narrowly rectangular, with semiannular bands red brown, common, sometimes incomplete, not forked, the radial walls with nodular thickenings sometimes present on both longitudinal and transverse walls.

Spores 13–13.9 µm, light brown, with a network of wide, irregular, coalescing vermiform ridges; spore:elater diameter ratio 1.8–1.9:1. Elaters tortuous, 6.7–7.2 µm wide, the spirals 2.4 µm wide.

DIFFERENTIATION—Affinities are with *C. parvispineus*, but *C. gippslandicus* differs from that species by the magnitude and distribution of surface echinae as well as by leaf polymorphism. The echinae are up to 3 cells long (Fig. 75: 14), often situated over the radial walls of leaf cells (Fig. 75: 14), but are absent from the ventral half of the leaf (Fig. 75: 1, 16) as well as gynoecial bracts and perianth surfaces (Fig. 75: 8). Echinae of *C. parvispineus* are mostly unicellular, juxtaposed over the cell lumen and occur throughout the dorsal surface of leaves as well as on bract and perianth surfaces. Also, leaves of *C. gippslandicus* are polymorphic and undivided or short bifid (Fig. 75: 1, 4, 5), while those of *C. parvispineus* are consistently bifid.

VARIATION—Shoots are polymorphic with regard to form, margin armature and surface ornamentation of leaves. Considerable variability often occurs within one population; a single shoot of *Engel 16793* serves as an example. The distal sector has the facies of *C. semiteres* with leaves that are undivided, entire (or with an isolated tooth at the apex) and the dorsal surface smooth (Fig. 75: 1). The median sector also has the facies of *C. semiteres*, but has hispid leaves (Fig. 75: 1). The basal sector has the facies of *C. rupicola*, the leaves having apex and dorsal margin armature similar to that species (but the leaf surface is hispid) (Fig. 75: 1). Other shoots of *Engel 16793* mostly have main shoot leaves strongly armed at the apex and dorsal margin (the apex often being short bifid) and the leaf surface hispid (Fig. 75: 16). Such leaves occur throughout the main shoot, although the basal leaves are more densely hispid. Branches, however, have smooth leaves (Fig. 75: 16). I have examined several specimens that consist all or mostly of this phase.

Another phase, exemplified by *Engel 15541* from Tasmania and *Engel 17055* from Victoria, Australia, consists of the complete shoot having a strong resemblance to *C. semiteres*. Most leaves (particularly those in the basal sector of the shoot) have surface armature.

Occasional populations consist of shoots that are mostly smooth-leaved, with some leaves merely sparsely hispid. In such cases verification of surface armature should be made under the compound microscope. Several shoots should be checked, particularly if other characters of *C. gippslandicus* are present, such as facies of *C. semiteres* in dorsal and ventral views, armed leaf apices and margins, etc. An example of the sparsely armed variant is *Verdon 1544*.

Trigones vary at the population level. Some populations have small to medium to at most feebly bulging trigones, while others have medium to knot-like trigones (Fig. 75: 15).

NOTE—Care should be taken in establishing the absence of ventral surface echinae. I have examined several collections that in profile under the dissecting microscope appear to have several surface echinae. Such structures are actually short, erect branches from prostrate aseptate hyphae of a fungus occurring on the leaf.

NOTES ON TYPE SPECIMEN—*Lophocolea lauterbachii* Steph. The protologue cites two localities and collectors—"Australia. Gippsland (*Lauterbach*); Tasmania (*Weymouth*)." I have studied the Lauterbach collection at G.

Entire shoots resemble *C. semiteres* in both dorsal and ventral views, with minimal change in facies from distal to basal sectors. Distal leaves are predominantly smooth, but median as well as basal leaves have the dorsal half hispid. Some shoots have the apex and margins of leaves sparingly armed, while others have the apex, dorsal margin, and to a lesser extent the ventral margin decidedly spinose-dentate. In both cases these shoots have greater leaf armature in median and basal sectors. Stephani notes this difference in armature, remarking, "folia superiora et ramulina saepe integerrima." Androecia and gynoecia are present; the latter are still included within the bracts.

The specimen, which is corticolous, closely matches the protologue and is designated as the lectotype. Stephani's icon of the species (*Lophocolea* no. 179) is based on this specimen, and includes figures of a male bract and a juvenile perianth, both of which agree with the protologue.

I have not seen Weymouth collections determined as *L. lauterbachii* at G; those at HO are mostly *C. rupicola* or, (1 coll.) *C. semiteres*.

DISTRIBUTION AND ECOLOGY—The species has a sporadic distribution in Tasmania (200–600 m) and mainland Australia (Victoria, ca. 50 [Lake Tyers]–1450 m; A.C.T., 650–1200 m; New South Wales, 620–860 m).

In Tasmania, the species has a sporadic distribution between 200 and 600 m in forests in the eastern half of the island as well as the northeast. It occurs nearly exclusively in *Eucalyptus* forests, at times with an understory of *Atherosperma*, sometimes with an understory of *Olearia*. It may be found in shaded, well-drained sites, such as boulders (especially those with some soil accumulation), moist logs, bark, or, occasionally, soil of steep banks. The species exceptionally occurs in rich *Nothofagus cunninghamii–Eucryphia* forests (Keith River Road, SW of Meunna, *Engel 19694*).

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5, 7–12, 14, 16, from *Engel 16793*, Australia, Victoria, Great Dividing Range, just NE of Fernshaw and NE of Healesville; **6, 15,** from *Engel 17055*, Australia, Victoria, Mt. Buffalo Natl. Park, between reservoir and road turnoff to Mt. Dunn; **13,** from *Engel 15541*, Tasmania, summit ridge of Mt. Dial.)

On mainland Australia the species occurs primarily in lower to middle-elevation forests of *Eucalyptus*, often where there is a dominant understory of *Leptospermum*; or of *Acacia*, *Prostanthera*, and *Pomaderris*; or of *Olearia* and *Pomaderris*. The species often occurs in protected, damp gullies or valleys (at times associated with a watercourse) where it may be found on rotted logs or stumps, on tree ferns or *Acacia* or, less often, on clay banks. The species extends into the subalpine zone in Victoria, and occurs on soil in crevices of granitic boulders near streams or waterfalls.

SPECIMENS SEEN—**TASMANIA.** Blue Tier, *Rodway s.n.* as *L. heterophylloides*–c. ♂ (HO); along Scottsdale to St. Helens Highway, half mi. E of Parr Rivulet, ca. 300 m, *Norris 31881* (F); Betts Hill, 600 m, *Ratkowsky 77/148* as *L. muricata* (HO); Mt. Wellington, *Ratkowsky H 1383* as *L. muricata*–c. per., *78/124* as *L. muricata* (HO); ibid., Silver Falls, *Ratkowsky 80/75* (HO); ibid., Myrtle Gully, *Ratkowky s.n.* as *L. lenta*–c. ♂ (F); ibid., Lenah Valley Track, ca. 335 m, *Ratkowsky 77/147* as *L. muricata* (HO); New Town Rivulet, *Rodway s.n.* as *L. fissistipula* (HO); River Plenty, *Rodway s.n.* as *L. spongiosa*–c. ♂ (HO); near Jacques Creek, near end of Styx River Road, *Norris 29051* (F); foot of Mt. Roland, *Rodway s.n.* as *L. echinellus* (HO); Lake Barrington, 3 mi. N of Wilmot, *Norris 34044, 34076* (F); along River Leven, 1 mi. S of Leven Hill, ca. 200 m, *Norris 32481* (F); summit ridge of Mt. Dial, SSW of Penguin, SE of Burnie, 400 m, *Engel 15541*–c. ♂ (F); Keith River Road just N of Dip River, SW of Meunna, 235 m, *Engel 19694* (F). **AUSTRALIA. VICTORIA:** Dandenong Range, Sherbrooke Forest Park, near Kallista, E of Melbourne, ca. 1250 m, *Engel 16759* (F); Great Dividing Range, Maroondah Highway just NE of Fernshaw and NE of Healesville, *Engel 16793*–c. sporo. + ♂ (F); Mt. Macedon, 5 km SE of Woodend, 910 m, *Streimann 15464* (F); 12.5 km SW of Whitfield, 820 m, *Butler 15* as *L. semiteres* (CBG); Mt. Buffalo Natl. Park, between reservoir and road turnoff to Mt. Dunn, 20 mi. W of Bright, 1360 m, *Engel 17055* (F); ibid., Dickson's Falls, ENE of The Horn (Mt. Buffalo), 20 mi. W of Bright, 1450 m, *Engel 17091* (F); Don Road, near Mt. Donna Buang, *Meagher 1673* (F); O'Shannassy closed water catchment, near Warburton, *Scott* (F). **A.C.T.:** Tidbinbilla Nature Reserve, Red Hill Trail, 28 km SW of Canberra, 900 m, *Streimann 15290*–c. ♂ (CBG); Brindabella Range, Warks Road, 30 km WSW of Canberra, 1200 m, *Streimann 15308*–c. ♂ (F); Uriarra Forest, 20 km WNW of Canberra, 650 m, *Streimann 160A* (CBG). **NEW SOUTH WALES:** Head of Bourkes Creek, 13 km NE of Captains Flat, 860 m, *Streimann 15320* (CBG); Brindabella Valley, Bramina Creek, southern tablelands, 36 km SW of Canberra, 620 m, *Verdon 1544* as *L. semiteres*, *1546*–c. sporo. (CBG).

Chiloscyphus* sect. *Microlophocolea J. J. Engel & R.M. Schust.

Lophocolea sect. *Microlophocolea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 426. 1885. *Chiloscyphus* sect. *Microlophocolea* (Spruce) Engel & R. M. Schust., Nova Hedwigia 39: 410. 1985 (1984). Type: *Lophocolea liebmanniana* Gottsche

Plants with ventral-intercalary branches at least sometimes present; leaves with ventral surface (suboptimal plants aside) with teeth; underleaves often with scattered teeth on abaxial surface of both lobes and lamina; underleaf lobes with opposing teeth or cilia.

The section has two species, *C. villosus* and *C. muricatus*; for key see under subg. *Microlophocolea* (p. 181).

Chiloscyphus villosus (Mitt. ex Steph.) J. J. Engel & R. M. Schust.

Lophocolea villosa Mitt. ex Steph., Spec. Hep. 6: 299. 1922. *Chiloscyphus villosus* (Mitt. ex Steph.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 425. 1985 (1984). Lectotype (*nov.*): New Zealand, without specific loc., *Colenso 298* (G!); isolectotype: (BM!).

Lophocolea cinerea Herzog, Trans. & Proc. Roy. Soc. New Zealand 65: 352. 1935, *syn. cf.* Hodgson (1953). Holotype: New Zealand, North Is., L. Waikaremoana, Jan. 1931, *Hodgson 81* (JE!); isotype: (CHR!).

Plants with the general appearance of *C. semiteres* in dorsal view, soft, loosely creeping to stiffly ascending, pure pale green to pale yellow green to pale yellow brown, nitid when dry, when live the old, dead basal portion at times gelatinous and slimy; shoots medium, to 2.2 mm wide, suboptimal, ± flaccid plants to 4.6 mm wide. Branches rather common, of *Frullania* type (the half-leaf of same general shape as leaves) or lateral-intercalary type (and then lateral or ventral-lateral in position) or ventral intercalary, the lateral-intercalary and *Frullania*-type branches of about equal frequency, the ventral-intercalary branches less common. Stems smooth dorsally but the ventral surface with scattered ciliiform paraphyllia in well-developed plants; stems 12–13 cells high, the cortex poorly differentiated dorsally but on ventral side of stem consisting of 1(2) rows of smaller cells, the cortical and medullary cells thin walled. Rhizoids in tight fascicles from stem at immediate base of underleaves. Leaves distinctly inflated in appearance, subopposite to alternate, subhorizontal, strongly dorsally assurgent in basal portion, widely spreading, loosely imbricate, free dorsally, with orientation strongly succubous, the insertion strongly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells. Leaves with dorsal surface densely hispid, armed with 2–3(4)-celled, erect, elongate echinae with an elongate terminal cell (the more elongate ones 34–43 μm long), the point of insertion of echinae variable: either over the lumen or radial walls of lamina cells, the echinae sparing or absent at ventral base of leaf; ventral surface with ventral half armed with (2)3–4(5)-celled, erect, elongate echinae, the dorsal half smooth, the ventral surface armature sparing or absent on sporadic leaves in suboptimal plants. Leaves broadly and strongly convex, asymmetrically wide ovate to oblate, occasionally ovate-deltoid, clearly widest near base; apex undivided and broadly rounded or short bifid, the lobes (with or without associated sinus) plane, subequal, medium to broadly acute, terminating in a uniseriate row of (2)3–4 cells, the lobe margins with opposing 1(2)-celled sharp teeth, the apex otherwise with copious teeth and (often) several laciniate projections; dorsal margin straight to broadly and slightly rounded, plane to broadly deflexed, denticulate to the base by 1–2-celled teeth and (often) several spinose-dentate-laciniate processes, the base decurrent; ventral margin broadly and often quite strongly rounded, strongly and sharply reflexed to weakly revolute (the dorsal surface teeth then seen in profile), with copious teeth and cilia. Leaf cells with walls thin, trigones medium to large and bulging, median leaf cells 22–29 μm wide, 25–31 μm long. Oil-bodies in all nonspine-bearing cells, the surface echinae with terminal cell devoid of oil-bodies, the 1–2 basal cells may or may not have them; oil-bodies of lamina cells occupying fraction of cell lumen, hyaline and decidedly glistening, (3)4–5 per cell, coarsely botryoidal and appearing like clusters of grapes, distinctly and coarsely segmented, fusiform to elliptic to globose, 5.8–8.2 × 2.9–4.3 μm to 9.1–11.7 × 3.9–5.9 μm, the globose ones 4.3–4.8 μm to 5.2–5.9 μm in diam. Underleaves quite dissected in appearance, much smaller than leaves, 2.1–2.7× stem width, free or narrowly connate on 1 side, the insertion M- or inverted U-shaped, the underleaves slightly spreading, approximate to contiguous, with both abaxial and adaxial surfaces hispid by armature similar to those of leaves except sometimes branched, the armature sparing or absent in suboptimal plants; underleaves slightly concave (ventral view), ovate to ± rectangular, 2–4 lobed, the median sinus descending to (0.65)0.7–0.75 or deeper and then the lamina of only a few cells high; lobes slightly to strongly diverging, ventrally sulcate, caudate, terminating in a uniseriate row of several elongate cells, the lobe margins with opposing uniseriate teeth or cilia composed of elongate cells; lamina margins recurved, with abundant teeth, cilia, laciniae, and (often) accessory lobes, the base often appendiculate. Asexual reproduction absent.

Plants dioecious. Androecia appearing similar to those of *C. spinifer*, subfolious, on main shoot or elongate *Frullania*, or lateral-intercalary, or ventral-intercalary branches, initially terminal but eventually become intercalary; bracts subfoliaceous, similar to vegetative leaves in shape and general form except the bracts are 1) slightly to moderately smaller, 2) more coarsely armed at the margins, 3) a little more dorsally assurgent, and 4) have a dorsal pocket; bracts loosely appressed to bract immediately above, the abaxial and adaxial surfaces of saccate portion smooth, the saccate portion fused toward base with opposite bract, the distal portion of bracts with dorsal surface ornamented as in vegetative leaves, the apex mostly broadly rounded, less often short bifid, the ventral margin armed as in vegetative leaves; lobule rather small for bract size, the margin inflexed, crenulate and with numerous subpyriform slime papillae; antheridia solitary, the stalk 1-seriate. Gynoecia rare, with a woolly appearance, on main shoot and *Frullania* as well as lateral-intercalary branches, the branches of varying lengths, with or without vegetative leaves; subfloral innovations absent; vestigial stem perigynium present, rather fleshy, with 2–3 cycles of bracts and bracteoles inserted on the perigynium. Bracts of innermost series considerably larger than leaves, transversely oriented, sometimes feebly ventrally falcate, commonly erect and ensheathing perianth, the distal sector often sharply reflexed, the bracts free from one another, concave at least in basal sector, narrowly ovate, with both dorsal and ventral surfaces armed as in vegetative leaves; apices short bifid by sharply deflexed lobes, the lobes ± symmetrical, ventrally sulcate, sharply acuminate, the margins with opposing, sharp teeth; dorsal margin of lamina sharply reflexed, copiously irregularly spinose-dentate-laciniate, often with a pronounced lacinium near base; ventral margin of lamina plane to sharply reflexed, with armature similar to dorsal margin. Bracteoles of innermost series considerably smaller than bracts, free or connate on 1 side, plane or slightly concave (ventral view), narrowly to broadly ovate, the abaxial and occasionally the adaxial surfaces with echinae; apices 4–6-lobed to ca. 0.4–0.7 by caudate lobes fringed with opposing teeth or cilia, the median pair of lobes the largest; lamina margins ciliate-laciniate. Perianth with a woolly appearance, longly exserted beyond bracts, obscurely to distinctly trigonous, narrowly oblong to clavate, the surface densely hispid with echinae similar to those of dorsal surface of leaf or the armature ± ciliiform, the surface often also with armed, narrow, subcaudate, vertically oriented lamellae; perianth not to slightly expanding toward the wide, deeply 3-lobed mouth; lobes deeply bifid, the segments subcaudate-caudate, the segment margins with opposing teeth and cilia, the lobes otherwise densely spinose-dentate to laciniate-lobulate below level of segments; keelar wings short, low or lacking. Calyptra ca. 0.7 the perianth length.

Seta 9–10 cells in diam., with 24 rows of outer cells surrounding an inner core of cells averaging of similar size. Capsule ellipsoid, 945 × 700 µm to 1190 × 840 µm, the wall 4–5-stratose, 42–48 µm thick, the outer layer of cells equal to thickness of the 2–2.5 of interior strata; outer layer of cells rather small, subquadrate to short rectangular, the radial walls with red-brown nodular thickenings, the thickenings mostly on longitudinal walls and to a lesser extent on transverse walls; intermediate and inner layer of cells subequal in thickness, the intermediate layer with vertical thickenings often considerably tangentially extended, sporadically becoming semiannular; innermost layer of cells irregularly rather short to long rectangular, the longitudinal radial walls with continuous sheets of red-brown material, with semiannular bands present, pale or nonpigmented in median portion, often incomplete, sporadically forked, the radial walls with distinctly pigmented, magenta, nodular to spine-like thickenings often present on both longitudinal and transverse walls.

Spores 13.5–15.4 µm, pale brown, with faint, dense, low, close, papillose and sporadic short-vermiculate markings, the spore:elater diameter ratio 1.3–1.8:1. Elaters rather tortuous, 8.2–10.1 µm wide, the spirals 2.4 µm wide.

DIFFERENTIATION—This species, like *C. gippslandicus* of Tasmania and Australia, has the surface echinae juxtaposed over both the lumen and radial walls of lamina cells (Fig. 77: 2, 3). It differs from that species by the characters in the key. Also, *C. villosus* has leaves that have an inflated, billowed-out aspect, a condition not found in *C. gippslandicus*.

VARIATION—The relative development of surface echinae appears to be an indicator of the relative vigor of the plants. Optimal plants have leaves with crowded echinae on the dorsal surface and with many echinae on the ventral surface (Fig. 76: 3, 6) (but see below). The leaves of such plants have margins copiously armed, and apices with 2 well-developed lobes possessing opposing sharp teeth (Fig. 76: 6, 7). Underleaves of well-developed plants often are 4-lobed, the lobes are ventrally sulcate and have opposing teeth or cilia (Fig. 76: 3), and the abaxial and adaxial surfaces are hispid (Fig. 77: 8, 9).

Echinae of the ventral surface of leaves and both surfaces of underleaves should be searched for with care. While presence *vs.* absence of such armature is a valuable taxonomic character, occasionally they are relatively sparse and inconspicuous or absent altogether on sporadic leaves and underleaves of shoots that otherwise are relatively vigorous, as in, e.g., *Engel 17625* and *Engel 23081*, both of which consist of plants with copious dorsal surface echinae and marginal armature as well as a high incidence of 4-lobed underleaves. Therefore, several leaves and underleaves should be carefully examined on each shoot studied.

Weaker plants have dorsal surface echinae more sparsely developed and with only a few echinae on the ventral surface (Fig. 78: 2). The leaf margins are sparsely armed, and the apices are notably variable: obliquely truncate and entire to 1- or 2-lobed. If shallowly bifid, the lobes often are of unequal size and shape. They may vary from sharp to rounded and the lobe margins are either sparsely toothed or entire (Fig. 78: 2, 3). The leaf apices otherwise are at most sparsely toothed. Suboptimal plants have underleaves usually 2-lobed and often shallowly divided, the sinus sometimes descending to only ca. 0.5. (Underleaves divided to ca. 0.5, however, are an extreme, and more deeply divided individuals are frequently present.) Underleaf lobes are plane and either sparsely armed or, more often, entire (Fig. 78: 3). The underleaf surfaces are smooth or occasionally have a few echinae (Fig. 78: 3). Examples of suboptimal plants are *Engel 17554*, *17732* and *Schuster 49113*. *Engel 17554* is an interesting variant. The plants were somewhat flaccid and very large for the species, being 3.4–

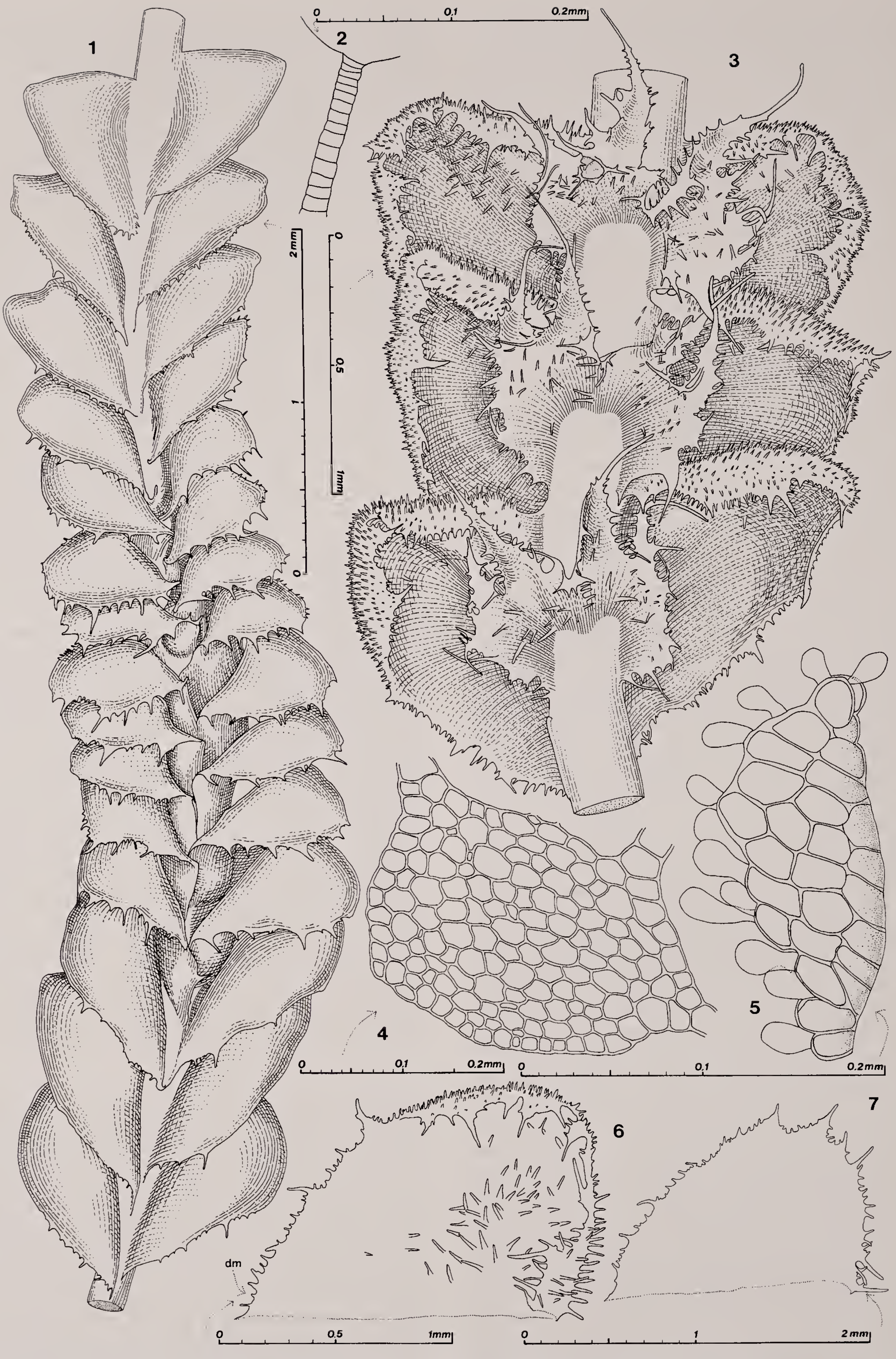

FIG. 76. *Chiloscyphus villosus* (Mitt. ex Steph.) J. J. Engel & R. M. Schust. **1.** Shoot with androecium, surface teeth omitted. **2.** Antheridium. **3.** Portion of shoot, ventral view. **4.** Stem, cross section. **5.** ♂ Bract, free dorsal margin of lobule. **6.** Leaf, ventral view (dm = dorsal margin). **7.** Leaf outline, surface teeth not shown. (All figures from *Engel 17973*.)

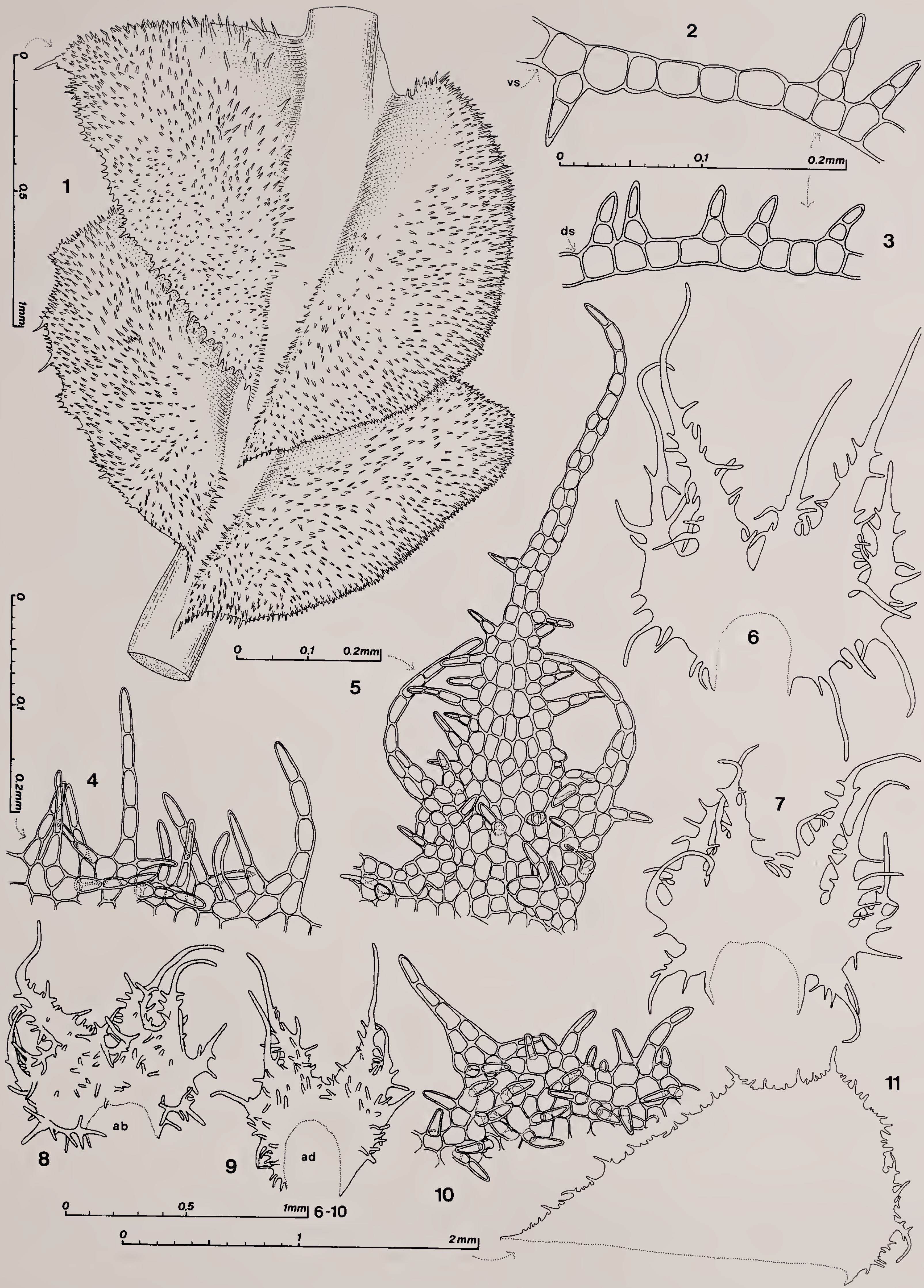

FIG. 77. *Chiloscyphus villosus* (Mitt. ex Steph.) J. J. Engel & R. M. Schust. **1.** Portion of shoot, dorsal view. **2.** Section through portion of leaf (vs = ventral surface). **3.** Section through portion of leaf (ds = dorsal surface). **4.** Basal portion of ventral margin. **5.** Median lobe of underleaf (abaxial surface). **6, 7.** Underleaves (surface teeth not shown). **8.** Underleaf, abaxial (= ab) view. **9.** Underleaf, adaxial (= ad) view. **10.** Portion of leaf apex including segment. **11.** Leaf (surface teeth not shown). (All figures from *Engel 17973*, New Zealand, South Is., Mt. Aspiring Natl. Park.)

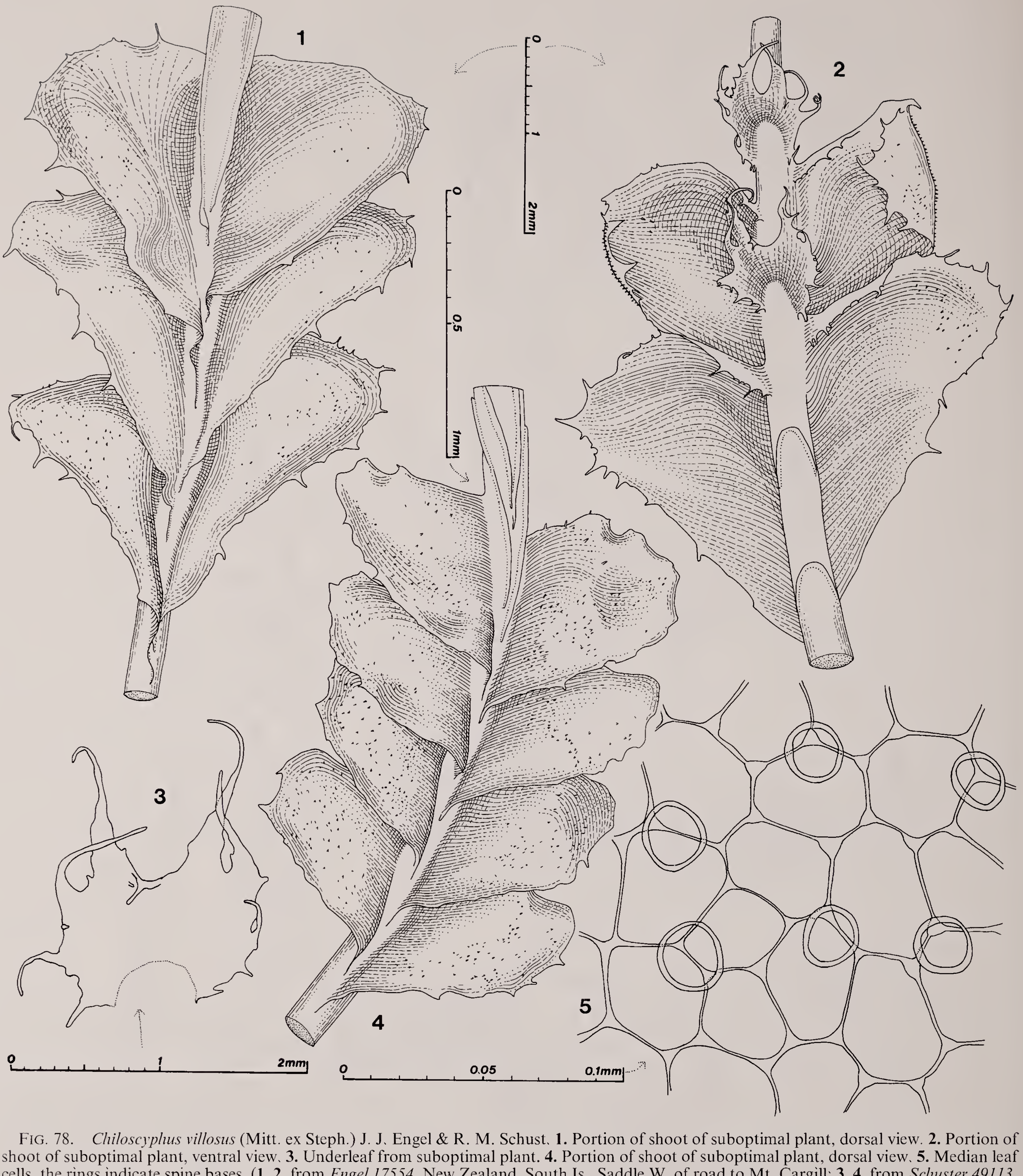

FIG. 78. *Chiloscyphus villosus* (Mitt. ex Steph.) J. J. Engel & R. M. Schust. **1.** Portion of shoot of suboptimal plant, dorsal view. **2.** Portion of shoot of suboptimal plant, ventral view. **3.** Underleaf from suboptimal plant. **4.** Portion of shoot of suboptimal plant, dorsal view. **5.** Median leaf cells, the rings indicate spine bases. (**1, 2,** from *Engel 17554*, New Zealand, South Is., Saddle W. of road to Mt. Cargill; **3, 4,** from *Schuster 49113*, New Zealand, North Is., Schormann's Track; **5,** from *Engel 17973*, New Zealand, South Is., Mt. Aspiring Natl. Park.)

4.6 mm wide. They grew among *Juncus* in an open, wet, boggy area (with abundant *Juncus squarrosus*, *Coprosma*, *Leptospermum*, and *Cassinia*).

Populations with leaves possessing only a few sporadic surface echinae among leaves that are completely smooth are particularly difficult, and unless a careful search is made for surface armature, such plants will key elsewhere. Suboptimally armed phases occur in particularly wet loci; *Engel 17740*, for example, was submerged in a pool, and *Engel 17744* occurred on saturated peaty soil. In view of these difficulties, I have placed such variants in the key to Australasian taxa with undivided leaves. Surface teeth of such suboptimally armed plants may be observed by carefully manipulating the leaves to provide a profile view. Stem paraphyllia are best seen by examining shoots under the compound microscope.

The sparsely armed phase easily may be confused with several other species. It superficially resembles *Chiloscyphus semiteres* with respect to: a) stature; b) broadly convex leaves that are initially dorsally assurgent, but ultimately deflexed; and c) deeply divided underleaves on each side with a prominent lateral process. It differs from that species by the polymorphous leaf apices, at times being bilobed, the ventral margins of leaves occasionally with 1(2) teeth, and the concave underleaves. *Chiloscyphus semiteres* has bilobed leaves only on suboptimal plants, uniformly entire leaf margins, and convex underleaves.

The polymorphous leaf apices and underleaf form of this phase bring to mind *Lamellocolea granditexta* (Engel, 1991c). Leaf cell characters will immediately distinguish these species: *C. villosus* has smaller cells (22–29 µm wide × 25–31 µm long) and medium to large trigones vs. cells 38–53 µm wide × 43–70 µm long and with trigones minute to small in *L. granditexta*. Polymorphous leaf apices also occur in *C. novaezeelandiae*; see discussion under that species (p. 77), and the key to taxa with undivided leaves (p. 11).

Notes—Some of the important taxonomic features of this species are at times difficult to observe. Surface echinae of the underleaves, for example, sometimes are difficult to see on underleaves *in situ*. Such teeth, however, are easily seen on underleaves that have been removed, when viewed with the dissecting microscope (Fig. 77: 8, 9). As above mentioned, care also should be taken with search for teeth on the ventral surface of leaves.

Notes on Type Specimens—1) *Lophocolea villosa* Mitt. ex Steph. The specimen at G (*Colenso 298*) consists of 6 shoots. The stem ventral surface is rather copiously armed with conspicuous hair-like paraphyllia (Stephani uses the term "capilliformibus" to accurately describe such paraphyllia). The dorsal and ventral surfaces of the leaves, as well as the abaxial surface of underleaf lobes and lamina, are distinctly hispid. A few androecium-bearing shoots are present. *Colenso 298* at BM is the source of the specimen at G. The BM collection consists of *Lophocolea villosa* intermixed with numerous shoots of the moss *Hypnum* sp. I selected the specimen at G as the lectotype. The specimens of *Colenso 298* represent a vigorous phase of the species.

Stephani's icon of the species (*Lophocolea* no. 178) shows a figure of a stem and attached leaf that is quite misleading, since stem armature is short, spine-like and appears much like that of *Cyanolophocolea echinella*. The much longer hair-like paraphyllia were poorly drawn by Stephani.

2) *Lophocolea cinerea* Herzog The dorsal surface of the leaves is rather copiously armed with echinae that are composed of 2–3 cells and that are juxtaposed either over the lumen or radial walls of the subtending lamina cells. The ventral surface rarely and sporadically has 1 to several echinae. Underleaf lobes are entire or armed with a tooth; only occasional lobes possess two opposing teeth. Abundant young gynoecia are present; the perianth extends to the level of the bract apices or just beyond. Trigones are small. The specimen represents a suboptimal expression of *C. villosus*.

Distribution and Ecology—Endemic to New Zealand (Stewart Is., South Is., North Is.), the species ranges from 120–1040 m and has a rather broad ecological amplitude. It is rather common in wooded areas, particularly in those that are less dense and thus permitting more light to lower reaches of the forest. It may be found in or at the margins of forests of *Nothofagus* (often *N. menziesii*), or scrubby (often rather open) areas of *Leptospermum ericoides* (kanuka) or *Leptospermum scoparium* (manuka) or *Podocarpus nivalis*. It frequently is terricolous (typically over a thick humus layer) or, at times, on rotted logs or over boulders or rocky outcrops. It also occurs in open boggy areas, with, for example, *Juncus squarrosus*, *Coprosma*, *Leptospermum* and *Cassinia* (500 m in Mt. Cargill area, *Engel 17549*), as well as over peaty soil or in pools in areas dominated by *Chionochloa* or *Chionochloa–Astelia* (490–825 m). In the Old Man Range it is terricolous in small boggy areas fed by small flushes in the alpine zone (1040 m, *Engel 23249*).

The species often tolerates quite exposed sites. For example, near the west shore of Lake Te Anau (immediately north of Ten Mile Bush), it is terrestrial in a low, rather open scrub dominated by *Leptospermum* with much of the floor covered by *Lycopodium*, bracken fern and the lichen *Cladina* (*Engel 23204*). In this connection the "Frost Flats" station is an interesting site (southwest of Minginui in South Auckland, *Engel 20748*). This is an open, low area with scattered *Leptospermum scoparium* and *Dracophyllum subulatum* with abundant *Cladina*. It is a rigorous habitat in a slight depression in the landscape that is subject to cold air drainage. Here *C. villosus* occurs terricolous in microniches receiving some protection by the scrubby vegetation. It may also occur in disturbed areas, such as under spruce (Conical Hill State Forest, Otago Prov., leg. *Allison*).

In the field, plants have a notable appearance in being soft textured, loosely creeping and pale yellow green to pale yellow brown. On vertical or subvertical substrates, such as rocky outcrops, the plants stiffly ascend, and are almost suberect in habit, with all shoot tips oriented toward the top of the outcrop. Likewise, when terricolous on slopes, plants are similarly stiffly ascending, with all shoot tips oriented toward the slope top.

Specimens Seen (selected)—**NEW ZEALAND.** Without specific loc., *Petrie 91* as *L. variabilis* (CHR). **STEWART IS.:** Without specific loc., *Murray 2253* (CHR); track to Mason's Bay, ca. 1–1.8 km W of Freshwater Hut/Landing, 5 m, *Engel, von Konrat & Braggins 24393* (F). **SOUTH ISLAND. SOUTHLAND:** Lake Hauroko, ca. 215 m, *Child H 1549* as *L. muricata* (F); Fiordland Natl. Park, along flat of Spey River, near W arm of Lake Manapouri, on Doubtful Sound Track, 190–230 m, *Schuster 52638* (F); ibid., Hope Arm Is., Lake Manapouri, ca. 185 m, *Johnson 136* (CHR); ibid., above Waiau River, near outlet of Lake Te Anau, *Allison 1409* (CHR); ibid., Cascade Creek, *sin. coll.* as *L. variabilis* (CHR); immediately N of Ten Mile Bush, near W shore of Lake Te Anau and ca. 20 km N of town of Te Anau, 200 m, *Engel 23204* (F); Fiordland Natl. Park, Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel 23208* (F); ibid., Falls Creek, near junction of Hollyford River road and Milford road, *Schuster 67-2436* (F); ibid., Esperance Valley, tributary of Cleddau River, N of Homer, 700 m, *Atkinson 13* (CHR); Hollyford River, Glacier Creek, 55 m, *Renner Hf/T4b* (AK). **OTAGO:** Catlins River area, Ajax Swamp, ca. 1 km N of Ajax Hill, *Child 5526, 5534* (F); Conical Hills Forest Plantation, near Tapanui, *Allison H 3657* (CHR); between Otokia and the coast, S of Dunedin, ca. 120 m, *Allison H 3656* (CHR); summit plateau of Mt. Maungatua, W of Mosgiel, 825 m, *Engel 17732, 17740* (F); same loc., 915 m, *Child 4101* (F); Dunedin, Town Belt, *Allison H 4885* (CHR); ibid., Cosy Dell, ca. 215 m, *Child H 1647* (F); W slope of Flagstaff, NW of Dunedin, 490–520 m, *Engel 18905*–c. ♂ (F); Flagstaff, NW of Dunedin, ca. 455 m, *Child H 1374* (F); Powder Creek Valley, near Whare Flat, *Allison 6658* (CHR); saddle W of road to Mt. Cargill, N of Dunedin, 500 m, *Engel 17549, 17554* (F); Onokonui Home area, Waitati, N of Dunedin, *Allison H 6414* (F); Old Man Range, Symes Road, 1040 m, *Engel 23249* (F); Fiordland Natl. Park, Humboldt

Mtns., above Lake Mackenzie, *Schuster 67-260* (F); ibid., Martin's Bay, N side of McKerrow River, *Hatcher 721, 845*–c. ♂ (F). **OTAGO/ WESTLAND PROV. BOUNDARY:** Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel 17973*–c. ♂ (F); near Haast Pass, *Mues NZ 17a* (F). WESTLAND PROV.: Lake Kaniere Scenic Reserve, Lake Kaniere, 152 m, *Engel, von Konrat & Braggins 24896* (F); Mt. Aspiring Natl. Park, 0.7 km N of Haast Pass and just S of Cross Creek, 525 m, *Engel 23090* (F). **CANTERBURY:** Arthurs Pass Natl. Park, Devils Punchbowl, *Stewart s.n.* as *L. muricata* (CHR); Arthur's Pass Natl. Park, Bealey Valley Track, Margarets Tarn, *Engel & von Konrat 27350* (F). **CANTERBURY PROV. BOUNDARY:** Lewis Pass Scenic Reserve, *Simpson s.n.* as *L. muricata* (CHR). **MARLBOROUGH NEAR BOUNDARY WITH NELSON PROV.:** Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, NE of St. Arnaud, ca. 700–920 m, *Engel 21444* (F). **NORTH ISLAND. WELLINGTON:** Wellington, Hawkins Hill, *Moss s.n.* (AK); N Tararua Mtns., Schormann's Track near Mt. Hines, 10–12 mi. W of Ekatahuna, ca. 610–915 m, *Schuster 49113* (F); NW Ruahine Range, vicinity between Makirikiri Tarns and Ruahine Corner Hut. 1100 m, *Engel & von Konrat 28102* (F); Tongariro Natl. Park, *Moore H 192* (CHR); ibid., Ohakune Mtn. Road, *Braggins s.n.* (AK); Taurewa, *Braggins s.n.* (AK). **GISBORNE:** Lake Waikaremoana, Ngamoko Track, ca. 610 m, *Hodgson 393* as *L. variabilis*, *394* (CHR), *s.n.* as *L. villosa* (F); between Lake Ruapani and Lake Waikare-iti, *Taylor s.n.* (AK). **SOUTH AUCKLAND:** Otanepu Bush, E of Taupo, ca. 670 m, *Allison H 3648* (CHR); "Frost Flats" on South Road between Totara Salvage Road and Wong Road, near Otupaka Stream, SW of Minginui, *Engel 20748* (F); Whirinaki Forest Park, road to Arahaki Lagoon, *Engel 20729* (F); Whirinaki State Forest, *Braggins s.n.* (AK); E of Taupo, ca. 670 m, *Allison H 540* (CHR); Kaingaroa Plains, Rotorua region, *Allison H 3649* (CHR); ibid., near Rangitaiki River, *Allison H 541* as *L. variabilis* (CHR); E of Waiotapu Valley, ca. 245 m, *Allison 3636*, *3639*, both as *L. variabilis* (CHR); near Rangitaiki River, above Murupara, near Rotorua, *Allison H 3647* (CHR); Ongaroto Road, near Atiamuri, S of Rotorua, *Allison H 3646* (CHR); near Atiamuri, S of Rotorua, *Allison H 61* as *L. variabilis, H 3650*, *H 3652*, *H 3653* (CHR). **CHATHAM IS.:** Northern slopes of Korako, ca. 100 m, *de Lange CH1050* (AK).

Chiloscyphus muricatus (Lehm.) J. J. Engel & R. M. Schust.

Jungermannia muricata Lehm., Linnaea 4: 363. 1829. *Lophocolea muricata* (Lehm.) Nees *in* Gottsche, Lindenb. & Nees, Syn. Hep. 169. 1845. *Chiloscyphus muricatus* (Lehm.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 419. 1984 (1985). Type: South Africa, Cape Prov., Table Mtn., *Ecklon* (*non vidi*).

Lophocolea hirtifolia Hook. f. & Taylor *in* Taylor, London J. Bot. 5: 366. 1846. Type: Tasmania, "with *Sticta chloroleuca*," 1832, *Lawrence s.n.* (BM!, FH!).

Lophocolea spiniflora Steph., Bull. Herb. Boissier 7(6): 481 (= Spec. Hep. 3: 181). 1907. Type: Africa, Mt. Runssoro, *Scott Elliott* (*non vidi*).

Lophocolea frappieri Steph., Bull. Herb. Boissier 7(6): 481 (= Spec. Hep. 3: 181). 1907. Type: Réunion, *Frappier*; Usambara, *Engler* (*non vidi*).

Lophocolea horridula Sande Lac., Ned. Kruidk. Arch. 3: 417. 1854. Type: Java, *Junghuhn* (*non vidi*).

Lophocolea liebmanniana Gottsche, Mexik. Leverm. 113. 1863 (Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh. II. 6: 209. 1868 [1867]). Type: Mexico, Hacienda de Mirador, *Liebmann* (*non vidi*).

Lophocolea hirta Steph., Bull. Herb. Boissier 7(1): 69 (= Spec. Hep. 3: 157). 1907. Type: Brazil, *Glaziou* (*non vidi*).

Lophocolea muricata var. β *laxior* Gottsche, Lindenb. & Nees, Syn. Hep. 703. 1847. Type: Mexico, "apud Mirador," *Liebmann* (*non vidi*).

Plants woolly in appearance, soft, loosely prostrate to closely adnate, pale green to yellow green to pale whitish green, often pale olive green in herbarium, nitid when dry, delicate; shoots small, to 1 mm wide. Branches common, of *Frullania* type (the half-leaf ovate-deltoid to deltoid) or ventral-intercalary type (the branch position varying from median ventral to (more often) ventral-lateral, the 2 types of about equal frequency. Stems smooth, without surface processes, 6–7 cells high, the cortex undifferentiated dorsally but on ventral side of stem consisting of somewhat smaller cells, both cortical and medullary cells moderately thick walled. Rhizoids large and thick walled for plant size, from stem in an ill-defined zone at base of underleaves, the tips often branched. Leaves varying from clearly alternate to subopposite, subhorizontal, somewhat to rather strongly dorsally assurgent at least in basal portion, spreading at ± 90° from stem, imbricate, free dorsally, orientation succubous to subtransverse, the insertion faintly recurved at ventral end, the lines of insertion extending to stem midline dorsally and thus not delimiting a leaf-free strip of stem cells; dried plants with little or no stem tissue exposed in dorsal view. Leaves with the dorsal surface, except near ventral base, densely hispid, armed with 1–3-celled erect, acute echinae which are juxtaposed 1 each over the lumen of most cells, the ventral surface with ventral half armed with 2–4-celled scattered, erect, elongate, acute echinae, the dorsal half smooth, the ventral surface armature sparing or (in suboptimal plants) absent; leaves strongly broadly convex, the apices deflexed and often oriented at ca. 90° with remainder of leaf, the leaves subsymmetrically broad ovate, clearly widest near base; apex bifid to 0.15–0.2, the lobes ± parallel to diverging, plane, equal or the ventral lobe larger and a little longer, the lobes medium-acute, terminating in a uniseriate row of 2–3 cells, the lobe margins with opposing 1–2-celled sharp teeth, the sinus broadly rounded to lunate; dorsal margin straight to faintly rounded, plane to slightly deflexed, copiously spinose-dentate to the base, the teeth 2–3 cells long and uniseriate, the margin not decurrent; ventral margin broadly and gently rounded, plane, copiously spinose dentate to ciliate-dentate to the base or nearly so, the teeth 2–3(4) cells long, mostly uniseriate but occasionally branched, somewhat longer than armature of dorsal margin. Leaf cells with walls moderately thickened, trigones small to medium and then the sides straight, median leaf cells without spines 14–18 μm wide, 17–19 μm long, the spine-bearing cells about the same size, 14–18 μm wide and 18–20 μm long. Oil-bodies (New Zealand populations) occupying conspicuous portion of cell lumen, hyaline, 2 or 2(3) per cell (with or without spines), the cells of spines lacking organized oil-bodies but have chloroplasts and may have oil-droplets, the oil-bodies of lamina cells papillose. Underleaves much smaller than leaves, 1.4–1.6× stem width, narrowly connate on 1 side, occasionally free, insertion symmetric, crescent shaped, the underleaves ± parallel with stem, distant, abaxial surface often with a few scattered ciliiform processes, the underleaves mostly cuneate, sporadically long rectangular, bifid to 0.75–0.8 or deeper and then the lamina of only a few cells high; lobes diverging or ± parallel, long-linear to subulate, terminating in a uniseriate row of several elongate cells, the lobe margins with opposing uniseriate cilia composed of elongate cells; lamina margins plane, with cilia that are often branched. Asexual reproduction absent.

Plants autoecious. Androecia rather short spicate, sometimes slenderly so, terminal or intercalary on leading shoots or moderately short to long ventral-intercalary or less often *Frullania*-type branches, the branches with at least several cycles of vegetative leaves. Bracts much smaller than leaves, erect to suberect, strongly dorsally assurgent, tightly appressed to bract immediately above, the abaxial surface of saccate portion dorsally smooth or with a few sporadic teeth, the ventral portion with several teeth, the adaxial surface of saccate portion smooth; bracts free dorsally, for the most part deeply ventricose except for the distal portion which is

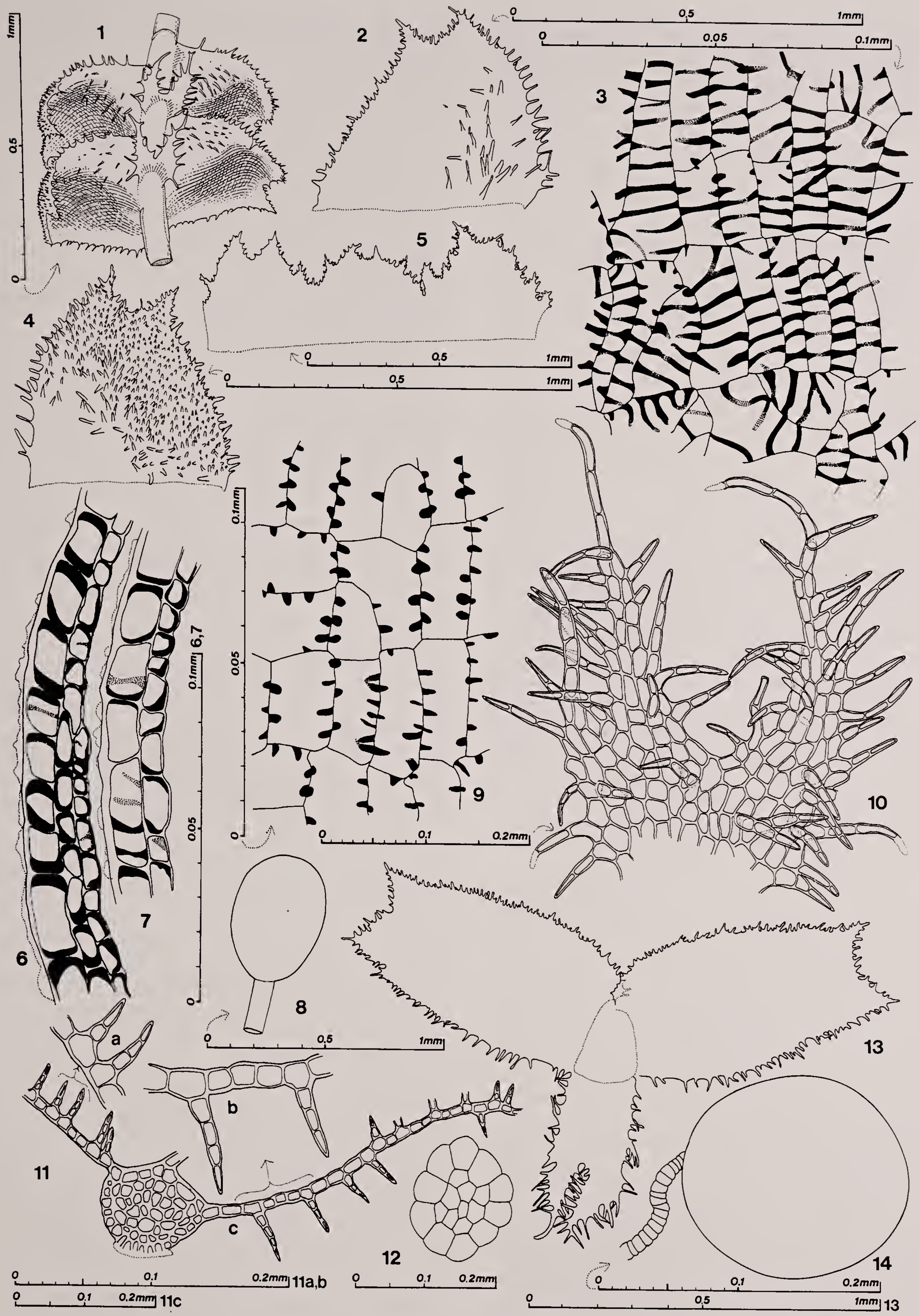

FIG. 79. *Chiloscyphus muricatus* (Lehm.) J. J. Engel & R. M. Schust. **1.** Portion of shoot, ventral view. **2.** Leaf, ventral surface (vm = ventral margin). **3.** Capsule wall, inner layer. **4.** Leaf, dorsal surface (vm = ventral margin). **5.** Perianth mouth, ventral lobe in middle. **6, 7.** Capsule wall, cross sections; amorphous substance on outer layer indicated with stipple. **8.** Capsule profile. **9.** Capsule wall, outer layer. **10.** Underleaf. **11.** Section through stem and portion of leaves, with sectors at higher magnification. **12.** Seta, cross section. **13.** ♀ Bracts and in middle bracteole. **14.** Antheridium. (All figures from *Engel 17688*, New Zealand, South Is., Morrisons Creek.)

abruptly and strongly reflexed, the distal portion bifid and with the dorsal surface ornamented as in vegetative leaves; ventral margin copiously dentate-ciliate to the base; lobule large for bract size, the margin strongly inflexed, distally with a sharp laciniiform projection which is armed with opposing, sharp, 1–2-celled teeth, the margin otherwise ciliate-dentate, the armature often terminating in a slime papilla; antheridia solitary, very large for bract size, the stalk uniseriate. Gynoecia on main axis and moderately short to long ventral-intercalary branches, the branches with at least a few cycles of vegetative leaves; subfloral innovations absent. Bracts of innermost series much larger than leaves, transversely oriented, obliquely to widely spreading, not to slightly appressed basally, free from one another, convex, elliptic, with both dorsal and ventral surfaces armed as in vegetative leaves; apices short bifid by sharply deflexed lobes, the ventral lobe a bit larger but not or hardly longer, the lobes broadly acute, with margins with opposing, sharp 1–2-celled teeth similar to those of leaf lobes; dorsal margin of lamina sharply reflexed and forming a cnemis, copiously spinose-dentate; ventral margin of lamina plane to slightly inflexed (the ventral-basal portion often with an elongate, shallow concavity), dentate-ciliate. Bracteoles of innermost series much smaller than bracts, ca. 0.35× bract area, very narrowly connate on 1 side, slightly convex (ventral view), oblong to rather narrowly ovate, the abaxial surface with cilia; apices bifid to ca. 0.4–0.5 by subcaudate lobes fringed with cilia; lamina margins ciliate. Perianth longly exserted beyond bracts, at least obscurely trigonous when young, but with maturity nearly cylindrical or at times somewhat dorsiventrally compressed, the perianths narrowly oblong to clavate, the surface, except for extreme base, densely hispid with echinae similar to those of dorsal surface of leaf; perianth not to slightly expanding toward the wide, distinctly 3-lobed mouth; lobes shallowly bifid, the segments medium acute to subacuminate, with margins spinose dentate as in leaves, the lobes otherwise lobulate and spinose dentate. Calyptra small, well included within perianth at maturity.

Seta 5 cells in diam., with 10 rows of outer cells surrounding an inner core of 9 scattered, much smaller cells. Capsule wide ellipsoid, 525 µm × 350 µm, the wall 2-stratose (and then 17–18 µm thick), the outer layer of cells often equal to 2× the thickness of inner layer) or 3-stratose (and then 20–22 µm, the outer layer of cells equal to thickness of the 2 interior strata); outer layer of cells rather small, subquadrate to subrectangular but not longly so, the radial walls thin, with red brown nodular to feebly spine-like thickenings, the thickenings mostly on longitudinal walls and only sporadically on transverse walls, the exposed tangential wall rather thickened and in surface view appearing smooth, but in cross section with a hyaline, amorphous substance without specific organization and not forming ridges; intermediate and, when present, inner layer of cells subequal in thickness, the intermediate layer with vertical thickenings often considerably tangentially extended, often becoming semiannular; innermost layer of cells irregularly rather short to long rectangular, the walls thin, semiannular bands red brown, common, narrow, nonpigmented in median or lateral portion or sometimes throughout, sometimes incomplete, sporadically forked, the radial walls with nodular to spine-like thickenings sometimes present on both longitudinal and transverse walls.

Spores 10.1–12.4 µm, pale brown, with faint, dense, low, close, papillose and sporadic short-vermiculate markings, the spore:elater diameter ratio 1.2–1.5:1. Elaters rather tortuous, 7.2–9.6 µm wide, the spirals 2.4–3.4 µm wide, rather closely wound.

Differentiation–Variation—The armature on the ventral surface of leaves is a valuable taxonomic feature. The only other hispid-leaved Australasian species with echinae on the ventral surface of the leaves is *C. villosus*. Characters of that species that will immediately separate it from *C. murcatus* are the larger plant size (to 2.2 mm wide), the shallowly bifid or (often) undivided leaves (vs. regularly and distinctly bifid in *C. muricatus*), the (ventral) stem paraphyllia and the 2–4-lobed underleaves. Presence of ventral armature on the leaves will distinguish the species from *Cyanolophocolea echinella*, with which it is rather commonly associated. The last has smooth leaves ventrally, a leaf-free gutter, and echinae on the dorsal surface of the stem.

Well-developed plants of *C. muricatus* have ventral surface echinae clearly visible under the dissecting microscope. However, the ventral surface echinae are sparingly developed or sometimes absent altogether in suboptimal plants. In such individuals the armature should be carefully searched for and confirmed with the use of a compound microscope. Large phases of *C. muricatus* often have sparse ventral surface armature, and therefore confusion is possible with *C. parvispineus*. Underleaf lobe armature and at least some echinae on the ventral surface of leaves will immediately distinguish *C. muricatus*.

Notes on Type Specimens—1) *Lophocolea hirtifolia* Hook. f. & Taylor The specimen consists of shoots that are rather flaccid, particularly in the basal half. Ventral surfaces of leaves are nearly uniformly smooth and exceptionally have an isolated echina.

Distribution—Pan-tropical to pan-south temperate; disjunct in Southern Appalachians. In Australasia the species occurs in New Zealand (South Is., 30–800 m [rarely higher]; North Is., 25–900 m); Australia: Tasmania (45–800 m), Victoria, New South Wales (860 m), Queensland (500 m).

Ecology—In Australasia *C. muricatus* is a species of rich, moist forests. It often has a wood substrate, and occurs, for example, on bark of living as well as dead trees or shrubs, rotten logs, stumps, exposed roots, and, on the forest floor, decayed bark, wood or twigs. It is also present on shaded rocks. In particularly humid situations it may be epiphyllous on fronds of *Blechnum*, *Trichomanes*, or *Hymenophyllum*, and may be locally common in this niche. It also occurs on the trunks and (occasionally) fronds of *Cyathea* and *Dicksonia*.

Specimens Seen (selected)—**NEW ZEALAND. STEWART IS.:** Port Pegasus, vicinity of Tin Range Track, ca. 100–200 m, *Engel, von Konrat & Braggins 24198* (F). **SOUTH ISLAND. SOUTHLAND:** S coast, 20 mi. NW of Riverton, ca. 150 m, *Child H 1640* (F); Lake Hauroko, ca. 120 m, *Child H 1554* (F). **OTAGO:** E face of Maungatua Range, *Allison H 1394*–c. sporo. (CHR); Dunedin, Town Belt, ca. 185 m, *Child H 1450* (F); ibid., ibid., Mornington, *Allison H 1393*–c. sporo. (CHR); ibid., Fraser's Gully, *Allison H 5550*–c. sporo. (CHR); Leith Valley, Morrison's Creek, outskirts of Dunedin, ca. 90 m, *Fife 6736*–c. per. (F); Morrison's Creek, N of Dunedin, 330 m, *Engel 17688*–c. sporo. (F); Ross Creek, Dunedin, ca. 185 m, *Child H 2348* (F); E slopes of Flagstaff Hill, *Allison H 5199* (CHR); Whare Flat, W of Dunedin, 70 m, *Engel 17635*–c. sporo. (F); Fiordland, head of Lake McKerrow, *Hatcher 887*–c. per. (UWM); Mt. Aspiring Natl. Park, Blue R. near confluence with Makarora R., NNE of Makarora, 310 m, *Engel 18906* (F). **WESTLAND:** Westland Natl. Park, Wombat Lake, track to Alex Knob, near Franz Josef Glacier, *Schuster 67-0390* (F); Camp Creek, W of Alexander Range, 450 m, *Reif C110* (F); Mt. Hercules Scenic Reserve, near Hercules Creek, off Route 6, *Engel 6567B*–c. per. (F); Paparoa Range, along Croesus

Track, ESE of Barrytown, 450 m, *Engel 19301* (F); Punakaiki, W side of Rte. 6, *Fife 4893* (F). **CANTERBURY/WESTLAND BOUNDARY:** Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski Area, *Engel 6472B* (F). **CANTERBURY:** Banks Pen., Price's Valley, 60 m, *Macmillan 77/209A*–c. sporo., *78/157A* (CHR); Mt. Cook Natl. Park, Governors Bush, SW of town of Mt. Cook, 760–800 m, *Engel 18220* (F); Christchurch, Riccarton Bush, *Macmillan 76/404* (CHR). **NELSON:** Paparoa Range, upper slopes of N side of Tiropahi or Four Mile R. between sea and Rte. 6, S of Charleston, 130–170 m, *Engel 19220* (F). **MARLBOROUGH:** Circular Track, Pelorus Bridge, *Braggins s.n.*–c. sporo. (AK); Kaiuma, Pelorus Sd., NNE of Havelock, ca. 30 m, *Child H 4459* (F); Seaward Kaikoura Range, Hinau Walk, W end of Mt. Fyffe, NW of Kaikoura, 210–240 m, *Engel 23277*–c. per. (F). **NORTH ISLAND. WELLINGTON:** Wellington, *Berggren s.n.* (CHR), *3781* (M); Keith George Memorial Park near Silverstream, Upper Hutt, *Mues NZ 17* (F); Wiltons Bush, ca. 90 m, *Child H 213* as *L. echinella* (F); ibid., Diels Path and Wall R. Path, *Mason s.n.*–c. sporo. (CHR); Elsden Reserve, Porirua, *Braggins s.n.* (AK); Akatarawa, Frances Stream, *Braggins 84/463B*–c. sporo. (AK); E Wairarapa, New Range Road, Big Hill, *Braggins s.n.* (AK); S of Wanganui R., near Turakina, *Allison H 3631* (CHR); Tongariro Natl. Park, ca. 7 km from Ohakune on Ohakune Mtn. Road, ca. 900 m, *Engel 21352* (F). **HAWKE'S BAY:** Without specific loc., *Beckett s.n.* (M); Wairoa, Kiwi, *Hodgson 41*–c. sporo. (CHR); Morere, *Hatcher 91*–c. sporo. (F); by Makaretu Stream, near Wairoa, *Hodgson 406* (CHR). **GISBORNE:** Near Lake Waikaremoana, Parkhurst, *Hodgson 83* (CHR); Lake Waikaremoana, *Hodgson s.n.* as *L. mittenii* (F); Poverty Bay, Panikau, *Sainsbury s.n.*–c. sporo. (CHR). **TARANAKI:** Mt. Egmont Natl. Park, near Stratford Mtn. Road, E slope of Mt. Egmont, ca. 610 m, *Schuster 48968* (F). **SOUTH AUCKLAND:** Roto-a-kui Bush, E of Taupo, *Allison H 3619*–c. sporo. (CHR); Whirinaki State Forest, Pigeon Camp, archeological site, E of Lake Taupo, *Braggins s.n.*–c. per. (AK); Whirinaki Forest Park, Waterfall Loop track, near Whirinaki River, *Engel 20685* (F); Pureora State Forest Park, Waipapa Ecological Area, 565 m, *Braggins et al. 134g*, *158j* (AK); plateau E of Waiotapu Valley, Rotorua county, ca. 550 m, *Allison H 3618* (CHR); E of Waiotapu Valley, S of Rotorua, ca. 520 m, *Allison H 3617*–c. per. (CHR); 40 Mile Bush, on Atiamuri–Taupo Road, *Allison H 3612*–c. per. (CHR); near Atiamuri, S of Rotorua, *Allison H 3626*, *H 3628* (CHR); Mangaiti Bush, near Atiamuri, S of Rotorua, ca. 490 m, *Allison H 3623* (CHR); Puaiti Bush, S of Rotorua, ca. 490 m, *Allison s.n.*, *H 3613*–c. sporo., *H 3633*–c. per. (CHR); Mamaku Plateau, W of Lake Rotorua on Rt. 5, 400 m, *Engel 20492*–c. per. (F); Ngongotaha Mtn., Rotorua, *Allison H 3621*–c. per. (CHR); Te Kauri Park, Kawhia, upper areas of Waikuku Valley, *Parkinson s.n.* (AK); Kauaeranga Valley, track between Table Mtn. Track and Moss Creek Hut Track, *Braggins s.n.* (AK). **NORTH AUCKLAND:** Hunua Ranges, Mangatawhiri Dam site, Auckland, *Braggins s.n.*–c. per. (AK); Waitakere Hills, W of Auckland, *Hatcher 201*–c. sporo., *1241*–c. per. (UWM); Swanson University Reserve, Tram Valley Road, 95 m, *Engel 20416*–c. per. (F); Swanson University Reserve, *Braggins s.n.*–c. per. (AK); Whitford, near Auckland, *Wornald 15* (CHR); NE Waitakere Ranges, Spraggs Bush, ca. 360 m, *Engel 22214*–c. per. (F); same loc., *Braggins s.n.*–c. per. (AK); Pohuehue Scenic Reserve, N of Auckland on State Highway 1, ca. 25 m, *Engel 21158*–c. per. (F); Rodney county, Albany Scenic Reserve, *Town s.n.* (AK); Logues Bush Scenic Reserve, 6 km NE of Wellsford, ca. 40–80 m, *Engel 20340*–c. sporo. (F); Waipoua Kauri Forest, *Hatcher 497* (UWM); Waipoua Forest, *Allison H 1613*, *H 1614* (CHR); Bay of Is. region, SW of Kerikeri, *Schuster 67-892* (F); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21095* (F); Mangamuka Range, 395 m, *Braggins 84/38b* (AK); ibid., Summit Lookout Forest, *Taylor 73/224* (AK); Mangamuka Gorge Reserve, N of crest, SE of Kaitai, ca. 305 m, *Schuster 67-1125* (F); Kiwanis Reserve, Junction of Okahu Stream and unnamed stream, ca. 5 km S of Kaitaia, N edge of Herekino Forest area, ca. 60–80 m, *Engel 20943* (F). **LITTLE BARRIER IS.:** Summit Ridge, *Braggins 84/205e*–c. per. (AK); Hingaia–Pohutukawa Flat, *Braggins et al. 80/899*–c. per. (AK). **TASMANIA.** E slope of Mt. Arthur, NE of Launceston, ESE of Lilydale, ca. 800 m, *Engel 15317* (F); Launceston, *E. Smith s.n.* (HBG); Adamson Peak, *Rodway s.n.* as *C. echinellus* (HO); Mt. Wellington, *Rodway s.n.*–c. per. (HO); ibid., McRobies Gully, *Rodway s.n.* as *C. echinellus* (HO); ibid., E facing slope, Fern Glade Track, ca. 460–520 m, *Engel 13044* (F); Castle Forbes Bay Rivulet, 305 m, *Weymouth s.n.* as *C. echinellus* (HO); Waterworks Gully, *Rodway s.n.* (HO); Cascades, *Rodway s.n.* (HO); Mt. Field Natl. Park, Russell Falls, *sin. coll.* as *C. echinellus* (HO); Gordon R. just E of confluence with Serpentine R., WNW of Strathgordon, 350 m, *Engel 13857* (F); ibid., vicinity of Sir John Falls, just up river from Butler Is., ca. 50 m, *Engel 14768* (F); Zeehan–Renison Bell State Reserve, on Murchison Highway 6.7 km N of intersection with road to Zeehan, 250–320 m, *Engel 20069* (F); Upper Meander R., *Rodway s.n.* (HO); waterfalls along Nietta Creek, "Castra Falls," off Gaunts Road, NE of Nietta, 415 m, *Engel 19841* (F); Newhaven Road, just S of Doughboy Hill, 0.4 km E of junction with Mawbanna Road, S of Port Latta, 45 m, *Engel 19726*–c. per. (F); vicinity of Trowutta Caves (Arch), 4.5 km by road from intersection of Reynolds Road and Reids Road, 6.9 km from Trowutta Post Office, ca. 180 m, *Engel 19757* (F). **AUSTRALIA. VICTORIA:** Great Dividing Range, Maroondah Highway, just NE of Fernshaw and NE of Healesville, *Engel 16795* (F). **NEW SOUTH WALES:** Head of Bourkes Creek, 13 km NE of Captains Flat, 860 m, *Streimann 15320* (CBG). **QUEENSLAND:** Lamington Natl. Park, trail to Elebana Falls, 500 m, *Thiers 1112* (NY).

Subg. *Spinoscyphus* J. J. Engel, subg. nov.

Caulibus paraphylliis bene evolutis saepe multiramosis praeditis, foliis 4–5-lobis, foliis amphigastriisque lobis vel dentibus primariis, secondariis tertiariisque pinnatiformibus.

TYPE—*Chiloscyphus trichocoleoides* Glenny, J. J. Engel & He-Nygrén

Stems with well-developed, often multiple-branched paraphyllia; leaves 4–5-lobed; leaves and underleaves with primary, secondary, and tertiary lobing or toothing in a pinnate form.

This monotypic subgenus, restricted to New Zealand, is unique in the genus in having leaves 4–5-lobed, the leaves and underleaves with primary, secondary, and tertiary lobing or toothing in a pinnate form and stems with well-developed, often multiple-branched paraphyllia. The species is highly isolated morphologically within the genus, and is therefore placed in its own subgenus.

Chiloscyphus trichocoleoides Glenny, J. J. Engel & He-Nygrén

Chiloscyphus trichocoleoides Glenny, J. J. Engel & He-Nygrén, J. Bryol. 31: 100, *f. 1, 2.* 2009. Holotype: New Zealand. Western Nelson Ecological Province, Marino Mountains, valley between Mount Owen and Mount Bell, 1440 m, *Glenny 9888* (CHR): isotypes: (F, H).

Plants ± anisophyllous, with a superficial similarity to *Trichotemnoma* or *Eotrichocolea*, fragile, soft and flexuous, feathery, with a woolly aspect, loosely prostrate, yellow-green, the leaf bases often deep olive green, the older, lower parts of plant pale brown, the shoots small, to 40 mm long, 1.2 mm wide. Branching frequent, irregularly and rather distantly pinnate, the branches mostly terminal, of *Frullania* type, most branches short (up to 3 mm long), truncate at their apices and lacking secondary branches, the primary branches sporadically moderately elongate and then with 1–3 secondary branches; branch half-leaf on main shoot somewhat basal to branch, composed of 1 lobe similar in form to dorsal lobe of leaf; first branch underleaf inserted on base of branch + main axis, 3–4-lobed, the lobes similar in form to those of underleaves; ventral-intercalary branches less common, originating in lateral half of underleaf axil, short or at times elongate and then becoming leading shoots. Stems with cortex in 1 (locally 2) rows of smaller, firm-walled cells, the exposed tangential wall thickened; medullary cells thin or feebly and indistinctly firm-walled. Paraphyllia common, varying from short cilia of only 2 cells grading to multiple-branched structures and then ± stellate and comprising up to ca. 17 cells; cells of cilia similar in shape to leaf lobe cilia. Rhizoids colorless, sparse, but always present, from stem at immediate base of underleaves, the tips digitate, nonseptate. Leaves alternate, loosely imbricate, very strongly succubously inserted (almost longitudinal), the insertion an inverted J-shape, the insertion lines not extending to stem midline dorsally and delimiting a leaf-free strip of 2 cells wide, the insertion strongly recurved ventrally and ending on the mid-lateral stem line; leaves concave, with the form of a loose cupulate basket, ca. 1000 µm from median point of leaf base to apex of ventral lobe, fundamentally bifid nearly to the base, but with 2–3 somewhat smaller accessory lobes so that leaves then appear 4–5 lobed, the lobes all incurved; dorsal lobe strongly erect, maximally pinnately incised-lobulate, each lobe with 3–4 pairs of opposed 1° lobules that become progressively larger toward lobe base and are oriented at 90°, the primary lobules in turn with smaller 2° lobules, the lobes ultimately dissolved into 2–3 pairs of opposed teeth or (at times) small 3° lobules, the dorsal lobe often with an accessory lobe toward base; ventral lobe similar to the dorsal lobe, with a prominent accessory lobe toward base. Lobes long attenuate-subcaudate, strongly canaliculate throughout, gradually tapering to a uniseriate row of 2–3(4) cells, the cells of the uniseriate row slightly thick-walled and slightly constricted at the septa, elongated only to ca. 3:1, the terminal cell rounded and not thickened at the tip; margins of lobes strongly recurved, profusely armed with pinnately-branching teeth, those near the apex oriented at ± 90° to the lobe, those lower on the lobes at ± 45°, the teeth ending in 1–2 elongated cells similar to those of the lobe apex; primary lobules canaliculate, similar in form to the lobes; sinuses between lobes sharply recurved. Disc asymmetric, highest in ventral half, ca. 5–10 cells high from leaf base to base of deepest sinus, the disc margins on each side with a few lacinia and cilia, the dorsal margin long-decurrent and with spinose teeth and (often accessory lobules) along the decurrency, the ventral margin reflexed. Cells of disc not in tiers, mostly isodiametric, hexagonal but in the lower median sector of main lobes becoming rounded-oblong, the walls thin, lacking intermediate thickenings, with trigones moderate (ca. 5% of cell area), bulging and knot-like, the cells 25–35 µm wide × 30–47 µm long; cells of lobes as in disc, isodiametric, with knot-like trigones; only the marginal teeth and cilia elongated; surface of leaves smooth throughout. Oil-bodies at mid-disc all of the same type, hyaline but appearing grey due to texture of surface, 4–7 per cell, irregularly finely papillose, at times appearing to have a fold or crease, the spherules projecting from membrane, the oil-bodies ovoid to nearly spherical, 6–10 × 4.5–6 µm. Chloroplasts ca. 3 µm in diam. Underleaves larger than the leaves, 1050–1225 µm wide × 875–945 µm long, free from leaves, bifid to ca. 0.9, but with 2 smaller lateral lobes, with all sinuses of about equal depth; lobes canaliculate by recurved margins, terminating in a uniseriate row of 3–4 at most moderately elongate cells, the tip cell capped by a slime papilla, the cilia and lacinia as in leaves; disc 6–8 cells high, plane (ventral view), the margins on each side with a few cilia and a small, accessory lobe. Asexual reproduction probably by fragmentation of terminal 1–2 cells of cilia.

Androecia and gynoecia unknown.

Distribution and Ecology—Known only from the type, which occurred on humic soil admixed with *Lepidogyna hodgsoniae*, with *Phyllothallia nivicola* and *Temnoma paucisetigerum* also present, and protected by a cover of dead leaves of *Chionochloa pallens* on the walls of a doline ca. 1 m deep and 1.5 m in diam. The doline is one of many on an alluvial surface about 300 × 200 m, situated in a large karst field. See Glenny et al. (2009).

Comments—Plants have a strong similarity to *Trichotemnoma corrugatum* (Steph.) R. M. Schust., the sole species encompassing Trichotemnomaceae R. M. Schust. of New Zealand and Tasmania (see Engel, 2005). A number of features are shared: the branches are of both terminal (*Frullania*) and ventral-intercalary types; the leaves are strongly succubously inserted, and are asymmetrically 4-fid, with smaller accessory lobes; the underleaves are deeply bifid and have small accessory lobes; the leaf and underleaf lobes are canaliculate; the margins of leaf lobes and lamina are armed with teeth that have a similar basic arrangement, i.e., orientation at right angles to the axis of the leaf; the rhizoids have the same origin and form, i.e., nonseptate and digitate at the tips; the stem cortex is in 1(2) layers of smaller cells with slightly thickened walls and medullary cells are thin walled; and the leaf cell trigones are well developed and are large and slightly bulging. *Chiloscyphus trichocoleoides*, however, differs from *T. corrugatum* in the lobulate leaf lobes, with each of the lobules in turn with small secondary lobules, which in turn are armed with teeth (Fig. 81: 1) vs. lobe margin with simple, elongate cilia in *T. corrugatum*. The oil-bodies are all of one type, whereas *T. corrugatum* is unusual in liverworts in having two types. The oil-bodies of *Chiloscyphus trichocoleoides* (Fig. 80: 5) correspond to neither type seen in *T. corrugatum*, being hyaline, but larger (6–10 µm long) than the hyaline oil-bodies of *T. corrugatum* (which are only 1–2 µm in diam.). The leaves and underleaves have smooth surfaces whereas in *T. corrugatum* they are striate-papillose. Stem paraphyllia are present (Fig. 80: 2, 3), while absent from *T. corrugatum*. The uniseriate row of the leaf lobes comprises 2–3(4) cells at most 3:1 (Fig. 81: 2, 3) vs. a uniseriate row of 5–8 elongate cells (to 8:1) in *T. corrugatum*.

Chiloscyphus trichocoleoides is similar in some respects to members of Trichocoleaceae, and in particular to *Trichocolea*. It is similar to *Trichocolea* in the following respects: branches are frequent and leafy throughout, i.e., not flagelliform; stem paraphyllia are present; the leaves are deeply dissected and asymmetrically 4-fid; oil-bodies are similar in size and hyaline; and rhizoids are digitate, while in *Trichocolea* and related genera they are rare. It differs from *Trichocolea* in the presence of ventral-intercalary branches vs. lacking in *Trichocolea*. Also, the leaf lobes are strongly canaliculate (Fig. 81: 1–3), a feature not seen in *Trichocolea*. The leaf and underleaf lobes of *C. trichocoleoides* have a uniformly 3-pinnate manner of division with armature diverging at ca. 90° (Fig. 81: 1), whereas in *Trichocolea* the leaf lobes divide in a mixture of pinnate and dichotomous styles. Disc cells are subisodiametric and have well-developed trigones (Fig. 80: 4) vs. elongated cells lacking trigones in *Trichocolea*. The leaf and underleaf surfaces are smooth vs. striate-papillose in *Trichocolea*. The underleaves are bifid (Fig. 81: 4), not equally 4-fid or bisbifid as in *Trichocolea*.

Chiloscyphus trichocoleoides is unique in *Chiloscyphus* in its leaf architecture, with the presence of primary, secondary and tertiary lobing or toothing in a pinnate form. Leaves are fundamentally bifid, but have 2–3 smaller accessory lobes and thus appear 4–5-lobed (Fig. 81: 1). Other divided-leaved species of *Chiloscyphus* are likewise fundamentally bifid but never have accessory lobes. Also, stem paraphyllia are distinct and well-developed, and are often multiple-branched

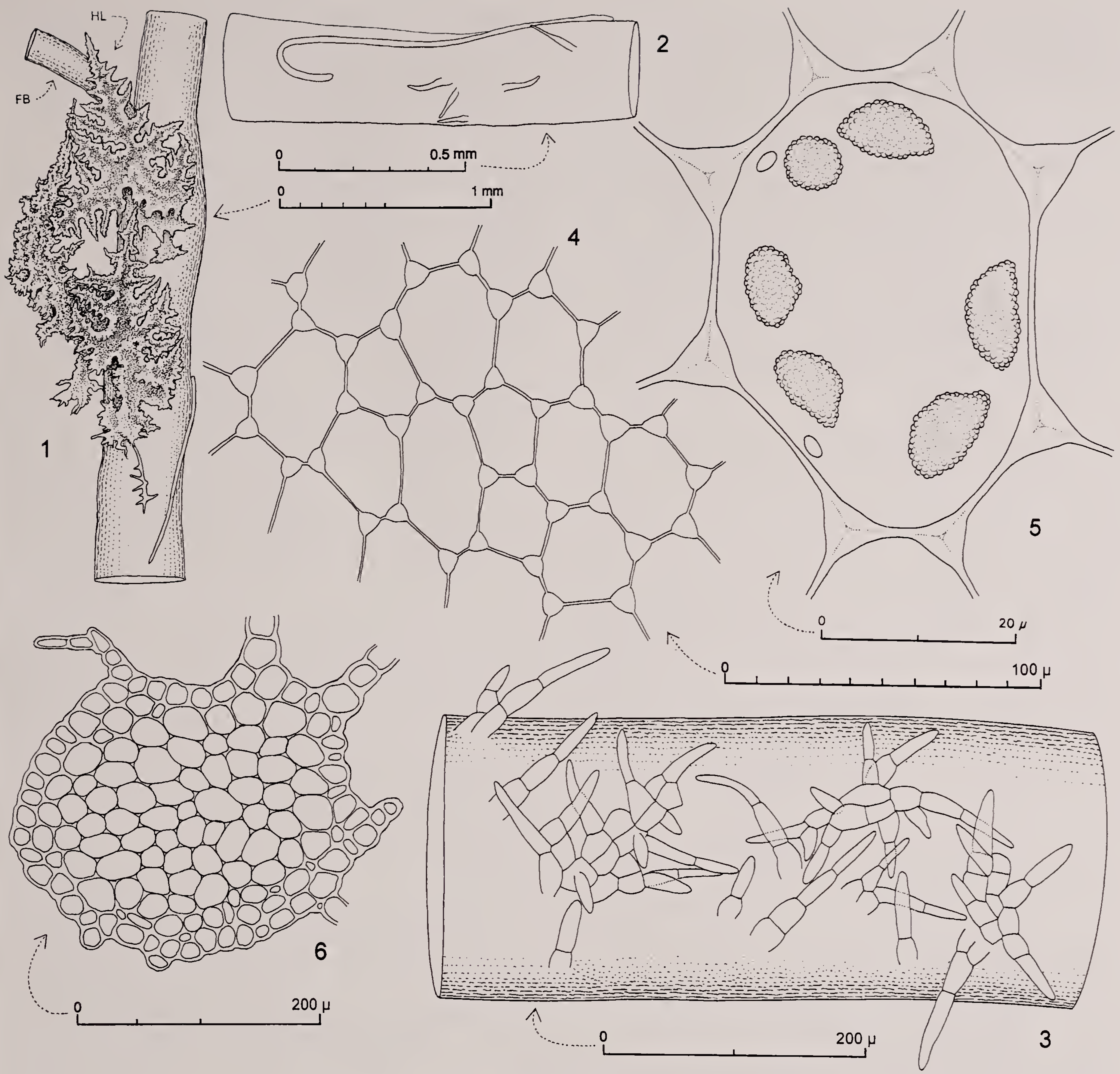

FIG. 80. *Chiloscyphus trichocoleoides* Glenny, J. J. Engel & He-Nygrén. **1.** Portion of leading shoot with a leaf, including a *Frullania*-type branch (= FB) and half-leaf (= HL) (dorsal view). **2.** Sector of stem showing insertion line, lateral view; note stem paraphyllia. **3.** Lateral aspect of stem showing paraphyllia. **4.** Median cells of leaf disc. **5.** Oil-bodies of median disc cell. **6.** Stem, cross section; note paraphyllia. (All from type.)

(Fig. 80: 2, 3) whereas in the rest of *Chiloscyphus* they are totally absent (except for ciliiform paraphyllia on the ventral surface of the stem in *C. villosus*). Within Lophocoleaceae the architecture of *Chiloscyphus trichocoleoides* is most similar to *Clasmatocolea trachyopa* (Hook. f. & Taylor) Grolle of southern South America. That species also has accessory leaf lobes, leaf lobes armed with teeth, leaf lobes canaliculate and terminating in a rather short uniseriate row, and leaf cells with well-developed trigones. *Clasmatocolea trachyopa* may be differentiated from *Chiloscyphus trichocoleoides* by the strongly adaxially concave leaves, the absence of secondary armature of the leaf lobes and the much smaller underleaves that are bifid to at most 0.5. The similarity in form and general architecture of the leaves in *C. trichocoleoides* and *Clasmatocolea trachyopa* is striking. Morphologically both represent highly isolated elements in their respective genera. In both genera leaf form otherwise is nearly uniformly simple. For example, *Chiloscyphus* has leaves either simple-bifid, divided normally to ca. 0.2, exceptionally to 0.4 or 0.5, or, less frequently the leaves are undivided. Leaves of *Clasmatocolea* typically are undivided and entire, and shallowly bifid only in a few species: *C. rigens* (Hook. f. & Taylor) J. J. Engel and *C. obvoluta* (Hook. f. & Taylor) Grolle, both of southern South America, and *C. inflexispina* (Hook. f. & Taylor) J. J. Engel of Australasia.

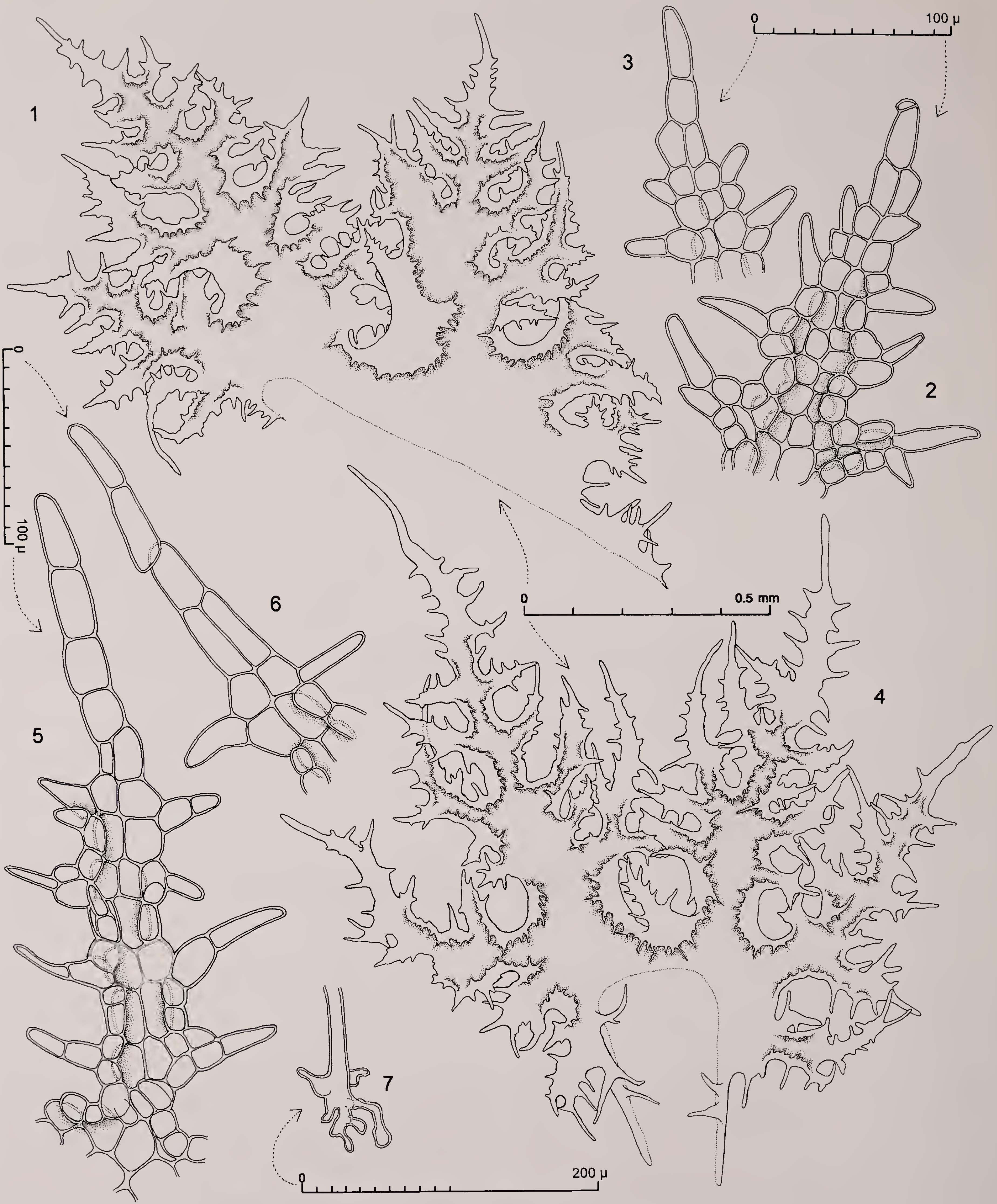

FIG. 81. *Chiloscyphus trichocoleoides* Glenny, J. J. Engel & He-Nygrén. **1.** Leaf. **2.** Distal sector of dorsal lobe of leaf, the tip cell lost. **3.** Distal sector of ventral lobe of leaf. **4.** Underleaf. **5, 6.** Distal sector of main lobe of underleaf. **7.** Rhizoid. (All from type.)

Chiloscyphus species excluded from Australasia or from genus

Lophocolea alternifolia (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 695. 1847. *Jungermannia alternifolia* Hook. f. & Taylor, London J. Bot. 4: 83. 1845. Lectotype (*fide* Engel, 1978): Falkland Is. (*non* New Zealand), *Lyall* (FH!) = *Chiloscyphus leptanthus* (Hook. f. & Taylor), J. J. Engel & R. M. Schust.

Reported for New Zealand by Hooker and Taylor (1845) and Weymouth (1903) for Tasmania. The species is included in the synonymy of *Lophocolea bidentata* by Hodgson (1953); see p. 45, this treatment. *Chiloscyphus leptanthus* occurs in the American sector (for range see Engel, 1990a).

Lophocolea connata (Sw.) Nees *in* Gottsche, Lindenb. & Nees, Syn. Hep. 153. 1845. *Jungermannia connata* Sw., Nov. Gen. Spec. Pl. Prodr. 143. 1788. *Chiloscyphus connatus* (Sw.) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 413. 1985 (1984). Type: Jamaica.

Reported by Gottsche, Lindenberg and Nees (1847) and Montagne (1845) for New Zealand (Auckland Is.). Fulford (1976) gave the range for *C. connatus* as West Indies, Mexico, Honduras, Colombia, Venezuela and Brazil.

Lophocolea divaricata Hook. f. & Taylor, London J. Bot. 5: 367. 1846, *non L. divaricata* Herzog, Arch. Esc. Farm. Fac. Ci. Med. Córdoba 7: 19. 1938. *Chiloscyphus divaricatus* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 414. 1985 (1984). Type: Chile, Prov. Magallanes, Isla Hermite, *Hooker* (NY!).

The species was placed in the synonymy of *L. bidentata* by Bastow (1888) for Tasmania and by Mitten (1854–55) and Hodgson (1953) for New Zealand. *Chiloscyphus divaricatus* occurs in the American sector (see Engel, 1978, 1990a); for range see Engel (1990a). See p. 45, this treatment.

Lophocolea echinella Lindenb. & Gott. *in* Gottsche, Lindenberg & Nees, Syn. Hep. 703. 1847. *Chiloscyphus echinellus* (Lindenb. & Gott.) Mitt. *in* Hooker f., Bot. Antarc. Voy. 2: 141. 1854. *Cyanolophocolea echinella* (Lindenb. & Gott.) Schust., Nova Hedwigia 72: 102. 2001. Type: New Zealand.

See Engel and He (2010).

Lophocolea latifolia Nees, Naturg. Eur. Leberm. 2: 234. 1836. *Chiloscyphus latifolius* (Nees) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 418. 1985 (1984). *Lophocolea bidentata* var. *latifolia* (Nees) Gil & J. Guerra, Collect. Bot. (Barcelona) 13: 178. 1982. Type: Europe.

Jungermannia bidentata L., Spec. Pl. 2: 1132. 1753. *Lophocolea bidentata* (L.) Dumort., Recueil Observ. Jungerm. 17. 1835, *non Chiloscyphus bidentatus* Steph., Hedwigia 32: 320. 1893. Type: Europe.

Reported as *Lophocolea bidentata* for New Zealand by Hodgson (1953, 1962), Hooker (1864–67), Mitten (1854–55), and Stewart (1978); for Tasmania by Bastow (1888), Carrington and Pearson (1888), Hodgson (1962), Mitten (1859), and Rodway (1916); and for Australia by Gottsche (1856). *Chiloscyphus bidentatus* is north temperate in range and, as indicated by Schuster (1980, p. 193), “reports from Cuba, from subantarctic islands (Possession I.; Kerguelen I.), and indeed from the entire Southern Hemisphere, remain questionable.” Within our area the species most often has been confused with *C. lentus*, *C. bispinosus*, *C. cuspidatus* and *C. subporosus*. See comments in text.

Lophocolea leptantha (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 694. 1847. *Chiloscyphus leptanthus* (Hook. f. & Taylor), J. J. Engel & R. M. Schust., Nova Hedwigia 39: 418. 1985 (1984). Type: Chile, Prov. Magallanes, Isla Hermite, *Hooker* (NY!).

The species was placed in the synonymy of *L. bidentata* by Bastow (1888) for Tasmania and by Mitten (1854–55) and Hodgson (1953) for New Zealand. *Chiloscyphus leptanthus* occurs in the American sector (see Engel, 1978, 1990a); for range see Engel (1990a). See p. 45, this treatment.

Lophocolea minor Nees, Naturg. Eur. Leberm. 2: 330. 1836. *Chiloscyphus minor* (Nees) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 419. 1985 (1984). Type; Germany.

The species is reported for New Zealand by Hodgson (1962). *Chiloscyphus minor* is “imperfectly holarctic” (Schuster, 1980, p. 227).

Lophocolea recurvifolia (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 693. 1847. *Jungermannia recurvifolia* Hook. f. & Taylor, London J. Bot. 3: 562. 1844 *non J. recurvifolia* Nees, Hepat. Javanicae 32. 1830. Lectotype (*nov.*): New Zealand, without specific loc., 1843, *Hooker* (FH!) (isolectotypes: BM![2]).

The species is included in the synonymy of *Lophocolea bidentata* by Hodgson (1953); see p. 45, this treatment.

NOTES ON TYPE SPECIMEN—The specimen is in rather poor condition—plants are very flaccid, and leaves are often incomplete. Underleaves are frequently absent but the complete ones I have been able to find have the form of *Heteroscyphus cuneistipulus*. The best developed leaves are bilobed and with distinctly acuminate segments. It appears that suboptimal leaves have the apex truncate to retuse. The dorsal and ventral margins of the leaf sporadically have a spine. I find no trace of sex organs. Two probably isolectotypes are at BM; both lack collector. The three original specimens studied are relatively pure, and consist of pale green shoots that are in particularly poor condition, and shoots that have dried yellow brown are in better condition. I tentatively place the specimen in the synonymy of *Heteroscyphus cuneistipulus*.

Lophocolea sabuletorum (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 697. 1847. *Chiloscyphus sabuletorum* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 422. 1985 (1984). Lectotype (*fide* Engel, 1978): Falkland Is., *Hooker* (FH!).

Lophocolea rivalis (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 701. 1847. Lectotype (*fide* Engel, 1978): Falkland Is., Port Louis, *Hooker* (NY!).

Lophocolea rivalis is included in the synonymy of *L. sabuletorum* by Hodgson (1953) and Mitten (1854–55) in treatments of New Zealand, and in the synonymy of *L. novae-zealandiae* by Bastow (1888) for Tasmania. *Chiloscyphus sabuletorum* is a species of the American sector (for range and synonymy see Engel, 1990a).

Lophocolea subviridis (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 699. 1847. *Chiloscyphus subviridis* (Hook. f. & Taylor), J. J. Engel & R. M. Schust., Nova Hedwigia 39: 424. 1985 (1984). Type: Chile, Tierra del Fuego, Cape Horn.

Lophocolea subviridis is included in the synonymy of *L. novae-zealandiae* by Bastow (1888), Hodgson (1953) and Mitten (1854–55). *Chiloscyphus subviridis* occurs in the Falkland Is. and southern South America (see Hässel de Menéndez, 1995).

Lophocolea tenax Steph. Spec. Hep. 6: 296. 1922. Type: New Zealand, without specific loc., *Petrie s.n.* (G!).

NOTES ON TYPE SPECIMENS—The leaves are long decurrent dorsally, and only a narrow strip of stem tissue is exposed in dorsal view. The ventral lobe of the leaf is longer than the dorsal. The underleaves, which are about as wide as the stem, are narrowly but distinctly connate on both sides. The underleaf lamina is of only a few cells high and the lamina has a tooth or lacinium but is otherwise entire. Some plants are tinged with purple (exceedingly rare in Lophocoleaceae). I tentatively place the species in the synonymy of *Heteroscyphus cuneistipulus*.

Lophocolea textilis (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hep. 696. 1847. *Chiloscyphus textilis* (Hook. f. & Taylor) J. J. Engel & R. M. Schust., Nova Hedwigia 39: 424. 1985 (1984). Lectotype (*fide* Engel, 1978): Falkland Is., *Hooker* (FH!).

Reported for New Zealand by Mitten (1854–55) and included in the synonymy of *L. bidentata* by Bastow (1888) and Hodgson (1953). The species occurs in the American sector (for range see Engel, 1990a). See p. 45, this treatment.

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